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THE ECOLOGY AND ENERGETICS OF APLYSIA JULIANA (QUOY AND GAIMARD, 1832).

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THE ECOLOGY AND ENERGETICS OF

APLYSIA JULIANA (QUOY AND QAIMARD, 1832)

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By

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ABSTRACT

The objectives of this study were: 1) to estimate recruitment rates for Aplysia juliana on a weekly basis throughout the year at two field locations on Oahu, Hawaii; 2) to examine the interrelationships between food intake, growth rate, maximum size and fecundity; 3) to establish an energy budget; and 4) to determine the interactions between recruitment, adult density, food density and season.

Recruitment occurred year-round although rates were higher in winter than in summer. Recruitment occurred in pulses which lasted from one to three days and the intensity of settlement varied between locations.

Aplysia juliana larvae settle on available species of the green alga Ulva and spend about three weeks feeding on the alga and growing before migrating to the adult habitat under rocks. Mortality while on the algae is very high and fewer than 2% survive to move to the adult habitat.

Maximum sizes of A. juliana attained under laboratory conditions were nearly five times larger than those seen in the field. Animals caged in the field grew rapidly until they reached sexual maturity when growth stopped. Animals raised in the laboratory continued to grow for several weeks after the onset of egg laying. This difference in growth pattern is attributed to limited access to food in the field imposed by their nocturnal habits and the activity-repressive response to heavy wave action.

Maximum sizes of animals in the field varied both between locations and within the same location at different times of the year. These differences were attributed to variation in alga density, temperature, and possibly variations in nutritional quality of the algae. Caloric content of U. lactuca from the Sand Island study site varied from 1850 to 3150 calories per dry gram.

Figured on a caloric basis, adult A. juliana, under ad libitum feeding conditions, allocated 10.69% of its nutritional energy into reproduction, 5.45% into somatic growth, 10.65% into respiration and 27.28% into feces over a 3½ month period. About 46% of the ingested calories were unaccounted for and were apparently lost to mucus production, excretion, and activity costs. Caloric assimilation efficiency was 72.7%, caloric net growth efficiency 22.2%, caloric gross growth efficiency 16.4% wet weight gross growth efficiency 23.6% and dry weight gross growth efficiency 10.95%.

The relative allocation to reproduction decreased when animals were raised on reduced food rations unless rationing was sufficiently low to prevent growth, in which case all energy above maintenance costs went to egg production. Caloric gross growth efficiency did not significantly change with lower rations.

At various field sites investigated, population numbers fluctuated greatly and frequent extinctions occurred. Aplysia juliana persists under such highly variable conditions by reaching sexual maturity early, and by producing millions of eggs over an extended reproductive life.

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CHAPTER I

General Introduction

Ecological investigations of shallow water marine habitats have tended to stress the roles of predators (Paine, 1965; Spight, 1974; Spight and Emlen, 1976) and sessile filter feeders (Connel, 1961, 1970; Crisp and Barnes, 1954; Seed, 1969; Weiss 1948), leaving relatively unexamined the activities of motile, algal-cropping herbivores. The flow of energy through ecosystems, a topic heavily explored in terrestrial habitats, has only recently been examined in littoral and near-littoral environments (Odum and Odum, 1955; Teal, 1957; Slobodkin, 1962; Paine, 1971, 1965). In the present study the biology of Aplysia juliana, an herbivorous marine gastropod, has been explored in both field and laboratory, to gain knowledge of such organisms and their particular role in the ecosystems they inhabit. An experimental approach has been utilized to provide explanations of varying growth rates, fluctuating population densities and energetic patterns which were observed.

Aplysia juliana is an opisthobranch gastropod mollusc in the family Aplysiidae. The species is easily identified by the prominent sucker on the posterior end of the foot. The species is found circumtropically; it has been reported from the eastern and western Atlantic (Marcus, 1955; Eales, 1960), as well as the Indian and Pacific Oceans (Eales, 1960; Kay, 1964). A. juliana can be found under rocks in shallow (0 to 2m), marine habitats characterized by the green algae Ulva. The habitats are usually rocky, exposed to wave shock, and are typically subject to fresh water runoff or seepage. Aplysia juliana occupies similar habitats

throughout its geographic range, although temperatures and algal diets vary considerably (Eales, 1960; Kay, 1964). While A. juliana is usually reported to feed on species of Ulva and Enteromorpha, Carefoot (1970) listed Cladophora sp. as a food species in Barbados and Saito and Nakamura (1961) stated that A. juliana in Japan prefer the brown alga Undaria pinnatifida. In Hawaii these animals feed only on species of Ulva.

There is confusion surrounding the taxonomy of the species of Ulva found in Hawaii. While U. reticulata and U. fasciata grow at several locations around the islands and are readily recognized, there is another type of Ulva present which resembles U. fasciata but is lighter in color, thinner and has a blade structure conforming to descriptions of U. lactuca. Presumably this alga is U. lactuca, a morphological variant of U. fasciata or a different species entirely. Aplysias fed this alga showed different growth characteristics than those fed U. fasciata. In this study this alga will be referred to as U. lactuca to differentiate it from the typical form of U. fasciata.

The life history of A. juliana is similar to that of many other opisthobranchs. Aplysia juliana has a planktotrophic veliger larval stage of about 30 days in laboratory culture (Switzer-Dunlap and Hadfield, 1977). Competent larvae settle and metamorphose on their food alga. The animals are simultaneous hermaphrodites although they function as only one sex during any particular mating. Long, spaghetti-like egg masses are laid on the bottom of rocks or on algae. Mating and egg laying occur many times during each animal's lifetime. These animals are nocturnal and do most of their feeding and spawning at night.

The objectives of this study were: 1) to estimate the rates of recruitment throughout the year at two locations, Sand Island and Kewalo Channel; 2) to examine the interactions between food intake, growth rate, maximum size, and fecundity; 3) to establish an energy budget; and 4) to determine the roles of algal standing crop and season in determining recruitment rate and population density.

Because of the interdependence of many of the experimental procedures it is difficult to separately analyze the results. Nonetheless, for organizational clarity the work is considered here under four main categories. Chapter II deals with the growth of juveniles and adults under a variety of conditions. The effects of different algal foods and different rations of food on growth are examined as well as the effects of light and water movement. Chapter III concerns recruitment of A. juliana from the plankton. Recruitment rates were monitored at two locations and related to algal standing crop, adult population size, fecundity, and season. Density, size distribution and fecundity are discussed in relation to algal abundance and recruitment rates in Chapter IV. Chapter V examines the energy budget under a variety of feeding conditions. Relative energy allocation between growth, reproduction, and maintenance is examined. Chapter VI concerns the life history of A. juliana how it has adapted to its habitat and how these patterns fit into generalized hypotheses on life history tactics.

CHAPTER II

Growth

Introduction.

Adult A. juliana grow to sizes of 50 g in Barbados (Carefoot, 1970), up to 450 g in Japan (Saito and Nakamura, 1961), and 60 g in Hawaii. Eales (1921) also reported animals of up to 300 mm in length, which would correspond to a weight of 400 to 500 g although she did not mention where she collected these animals. There are even large differences in adult sizes between populations on the island of Oahu. In addition, at any one location the maximum sizes attained at one time of the year are different from those at other times, and if Hawaiian animals are raised in the laboratory they can grow to almost 300 g.

Carefoot (1970) studied the growth and nutrition of A. juliana fed on several algal species on which the animals normally fed. He found considerable variation in the growth rates, absorbtion efficiencies, growth efficiencies, and fecundities of animals fed these different algae. Aplysia juliana in Hawaii feeds on several species of Ulva which are found at many different locations around the island. Growth and fecundity were monitored in animals fed on the different types of Ulva at ad libitum and lower rates in an attempt to mimic field sizes and, indirectly, to estimate the feeding rates of animals in the field.

Food abundance is but one of many factors which can affect the growth and maximum sizes of animals. Physical factors such as temperature, light and water movement can also indirectly affect growth in animals (Brown, et al., 1938; Drosser, 1955; Ebert, 1968; Van Heukelem, 1978). The effects of day-light and water movement on growth were tested in

the laboratory. Effects of temperature, however, were not tested. Where possible, growth experiments were conducted at 25° C. In Hawaii the water temperature varies only slightly 23-27° C). Because of the length of the adult growth experiments, some variation in ambient temperature occurred.

Methods.

Animals raised in the laboratory grew for longer periods of time and attained sizes five times larger than those found in the field. The following experiments were designed to determine growth rates and factors affecting those growth rates both in the field and laboratory: 1) growth of juveniles fed several types of Ulva in the laboratory and, in addition, short term growth experiments with juveniles in the field were performed for verification of these rates; 2) growth of adults in the field was measured on caged and uncaged animals in their natural habitat; 3) adult growth in the laboratory under ad libitum feeding conditions with various algal species; 4) laboratory studies of the effects of current on growth; 5) laboratory studies of the effects of light on growth; and 6) the effects of various reduced feeding rations on growth and maximum size.

1) Growth of Juveniles in the Laboratory. An age-weight relationship for juvenile A. juliana was established by growth studies conducted in the laboratory. Laboratory reared sibbling larvae were allowed to settle on each of four types of algae (U. reticulata and U. fasciata from Kewalo and U. reticulata and U. lactuca from Sand Island) in small finger bowls. Seawater in the bowls was changed every day and fresh Ulva

was added when necessary. Juveniles were transferred into mesh baskets suspended in flowing seawater tanks after about 10 days of growth. Growth was monitored as soon as juveniles were large enough to be safely weighed (.001 g) and continued until they reached about 10 g. Growth of two groups of juveniles on each alga was followed in the above manner. Several curves were fit to the growth data; the best fit was to the power function $Y = AX^B$, where X = weight, Y = age, A = y intercept and B = slope. From these curves daily growth intervals were calculated for animals on each algal type and thus age of any juvenile could be estimated from its weight if its algal diet were known.

Juvenile growth rates in the field were estimated by following the growth of cohorts after occasional, large but discrete recruitment periods. Mean weights for the juveniles in the cohort were calculated each week for as long as they remained on the algae.

2) Growth of Adults in the Field. Growth in the field was examined by placing animals in protective cages. A reinforced wire mesh cage .5 x .5 x .75 m was secured to the bottom at Sand Island by driving half meter sections of steel reinforcement bar into the rock. One-quarter inch diameter wire mesh did not hold up in heavy surf and had to be replaced by a screen of 1/16 inch thick galvanized expanded metal with 1/4 inch diamond shaped holes. A zink plate was attached to the steel frame to reduce corrosion. Ten to fifteen cm of sand and gravel covered the bottom mesh and the top was hinged to allow access to the animals inside. Four or five animals of about 1 g each were introduced for each experimental run. The cage served to protect the animals from predators

larger than 1/2 cm in minimum dimension and kept the experimental animals from escaping. Wave shock was reduced very little. At 7 day intervals the animals and spawn were weighed and fresh Ulva-covered rocks from the surrounding area were placed inside the cage. The animals were never allowed to run out of food and the experiments were continued until all the animals had died.

3) Tagging Experiments. Several methods of tagging were tested. Animals were heat branded with wires fashioned into small numbers. Individuals of various sizes from the field were branded, held in tanks for two days and returned to the field. Collections were repeated in the same area the next week. One group was kept in the laboratory to determine how long the brand remained legible and also to check for any adverse effects of the branding.

Animals branded and held in the laboratory survived well (none died) but branding must have greatly increased mortality in the field because branded animals were rarely recaptured. Scar tissue obscuring the brands was another problem and although it was possible to brand animals weighing less than 5 g, the brands soon became illegible as the animals grew. The populations of A. juliana in the areas where the animals were released were not large enough to assimilate the numbers of branded animals and result in such a small recapture.

A second form of individual tagging which had proved successful with A. kurodai in Japan (Nishiwaki et al., 1975) was also tested. This technique involved puncturing the posterior part of the foot with a small diameter enameled wire and tying a numbered tag to it. Many animals

of various sizes were tagged in this fashion and released at Sand Island and elsewhere. One set of tagged animals was also maintained at the laboratory for observation. Aplysia juliana, unlike A. kurodai, spends a large amount of its time either widged under rocks or buried in the gravel. This activity ripped out every type of tag that was tried.

Other forms of non-individualized tagging were tested to follow cohorts of seeded animals in the field. Coloring the animals with vital dyes and tatooing with india ink were all unsuccessful.

About 3% of the recruits found on algae in the field had a very conspicuous spotted color pattern. Several of these animals were collected, grown to maturity, mated, and their larvae reared through metamorphosis. Forty spotted juveniles averaging 2 g each, were released into a section of the Sand Island study area which had been previosuly cleared of other Aplysia. Their growth was monitored weekly for the first month and then monthly until all had died. The lack of the spotted pattern and small size allowed new recruits to be recognized and removed.

4) Adult Growth in the Laboratory. Animals used in laboratory growth experiments were small juveniles removed from algae collected in the field. Several small animals (usually under 1 g) as close as possible to the same size were chosen. There were always at least two animals and usually four or five in each experiment to allow for normal mating and egg production. Five seemed to be the maximum number of adult A. juliana that could be kept in a 100 liter tank with running

water. Algae were collected every two to five days depending on need and on the algal species being used. Ulva reticulata lasted longer than U. lactuca in the tanks and thus did not have to be collected so often. The animals were placed in shaded tanks with running seawater and algae were supplied ad libitum. In some studies the amount of food consumed was not measured; in others, at two day intervals remaining algae were removed and weighed, animals and spawn were weighed, and fresh damp-dried algae were added. Growth was monitored in the above fashion using U. reticulata, U. fasciata, and U. lactuca as food. Experiments lasted until the weights of the animals leveled off (usually about three months), or until they died.

5) Effects of Water Movement on Growth. The effect of current on growth was examined in two large circular cement tanks, 2.4 m in diameter and filled with water to a .5 m depth. One was equipped with two water jets to circulate the water clockwise at the edge of the tank. A circular, plastic mesh fence with 7 mm holes was erected .5 m from the edge to confine the animals to the area of fastest current; maximum current velocity was about 1 m per second. The second tank had the same total flow volume but the water was not directed in a way to cause a single strong current. Groups of 10 animals were placed in each tank and growth was monitored weekly. Food and shelter were supplied by including several Ulva covered rocks in each tank; the rocks were changed when the animals had eaten the algae. The experiment was run about three months when the animals had reached the characteristic growth plateau.

6) Effects of Light on Growth. In the field, A. juliana spends daylight hours either under rocks or buried in gravel. They become more active at night and can be seen crawling around and feeding. There is a suspicion that light might inhabit growth by causing the animals to bury and thus restrict their access to food. This behavior was not as evident in the laboratory where they would feed all day. Animals studied in growth experiments were kept either in indoor tanks where light levels were relatively low or in outdoor tanks where the animals were shaded both by partial covers on the tanks and by the large amounts of algae supplied as food.

Tests for the influence of light on growth were carried out in paired .31 x .46 x 1.22 m seawater tanks. Each tank had 15 cm of coarse gravel on the bottom in which the animals could bury, as well as several large rocks. The substrate was a fair approximation of that in the natural habitat. Both tanks were placed in an area that was exposed to direct sunlight for most of the day. In both tanks an ample flow of water prevented heating. One tank was painted black and its top was covered with two layers of black plastic. The other was left open to ambient light conditions. Five animals of about 1 g each were placed in each tank. The animals were fed ad libitum but algal quantities were kept sufficiently small so animals in the ambient tank were not appreciably shaded from the sunlight by the algae. Growth and fecundity were monitored weekly. Animals in the dark tank were exposed to short pulses of light every day when they were fed and/or weighed and there was probably some penetration of light through the plastic where the water hoses went through.

7) Effects of Feeding Levels on Growth. The effect of food availability on growth was tested in several ways: A) Food was restricted to a percentage of the rate that an animal fed ad libitum would eat. In this case the rationing started at an early size and age (under 1 g). B) Food was restricted after animals had reached sexual maturity. C) Food was rationed for only certain parts of the animal's life. D) Animals were given a small, constant amount of food from early in their life.

A) Food Restricted as a Percentage of Ad Libitum Feeding Rate. In order to calculate the amount of food to be given to the second experimental group, a curve of food consumption vs. age was constructed from ad libitum studies described earlier. The animals were fed at the rate the ad libitum animals ate as a function of their body size minus 25%. For example, if at the age of one month the ad libitum animals were eating 50% of their weight per day, the experimental animals would be fed 37.5% (50% x .75) of their body weight. A second ad libitum control was also run at the same time. Food consumption, growth and fecundity were monitored every two days and the experiment was continued for 3½ months.

B) Food Restricted after Sexual Maturity. Growth of caged animals was very rapid until the onset of egg laying at which time growth slowed and stopped. The early rates of growth were comparable to those on ad libitum rations in the laboratory. In an attempt to mimic this growth pattern, animals were allowed

to feed ad libitum until egg production began when they were put on rationed amounts of food. Twelve animals of about 1 g each were fed ad libitum until the first eggs appeared. The mean weight at this time was 40 g. Rationing was calculated as a function of this weight. The animals were divided into three groups of four and fed 10, 20, or 30 g of U. lactuca per animal per two days. Growth and fecundity were monitored for over three months when the animals began to show signs of senescence.

C) Food Restricted for Specific Periods. Several experiments were conducted to examine growth as a function of age and/or size. Twelve animals weighing 1 g each were selected and grown under the feeding conditions shown below:

12 animals

8 fed ad libitum to sexual maturity		4 starved for first 8 days of experiment
A	B	C
4 put on rations of 4 g Ulva/animal/2 days until group B reached and held maximum weight	4 continued ad libitum	Returned to ad libitum
Returned to ad libitum		
Maximum weight	Maximum weight	Maximum weight

D) Food Restricted to Small Constant Amount. The final experiment was to give animals a small fixed amount of food from very early in their life. Two small animals (.70 and .74 g) were fed

about 1 g of Ulva each every two days. The function of this experiment was to examine the relationship between sexual maturity, size, an/or age.

Results.

1) Growth of Juveniles in the Laboratory. An age-weight relationship was established as a means of aging recruits found in the recruitment studies. Growth of juveniles varied between the four algal types and is shown in Figure 1. Juvenile growth on each algal food was fit to several standard curves; the best fit was seen with the power function $Y = AX^B$ (Y = age, A = y intercept, X = weight, B = slope). As duplicate experiments on each alga produced very similar results with only small differences in slope and intercept, the data were lumped and fit again. From these curves daily growth increments were calculated for animals feeding on each algal species.

Growth rates for animals on the different algae varied to the extent that the time to achieve a weight of 10 g, for example, was 36 days for U. reticulata from Kewalo, 31 days for U. lactuca from Sand Island, 38 days for U. reticulata from Sand Island and 28 days for U. fasciata from Kewalo. Juveniles removed from the algae holding tanks were aged by the age-weight relationship described above, but since the algae were held for 14 days (for U. reticulata) or 7 days (for U. lactuca) after collection, this number had to be subtracted in order to get the age of the recruits at the time the algae were collected.

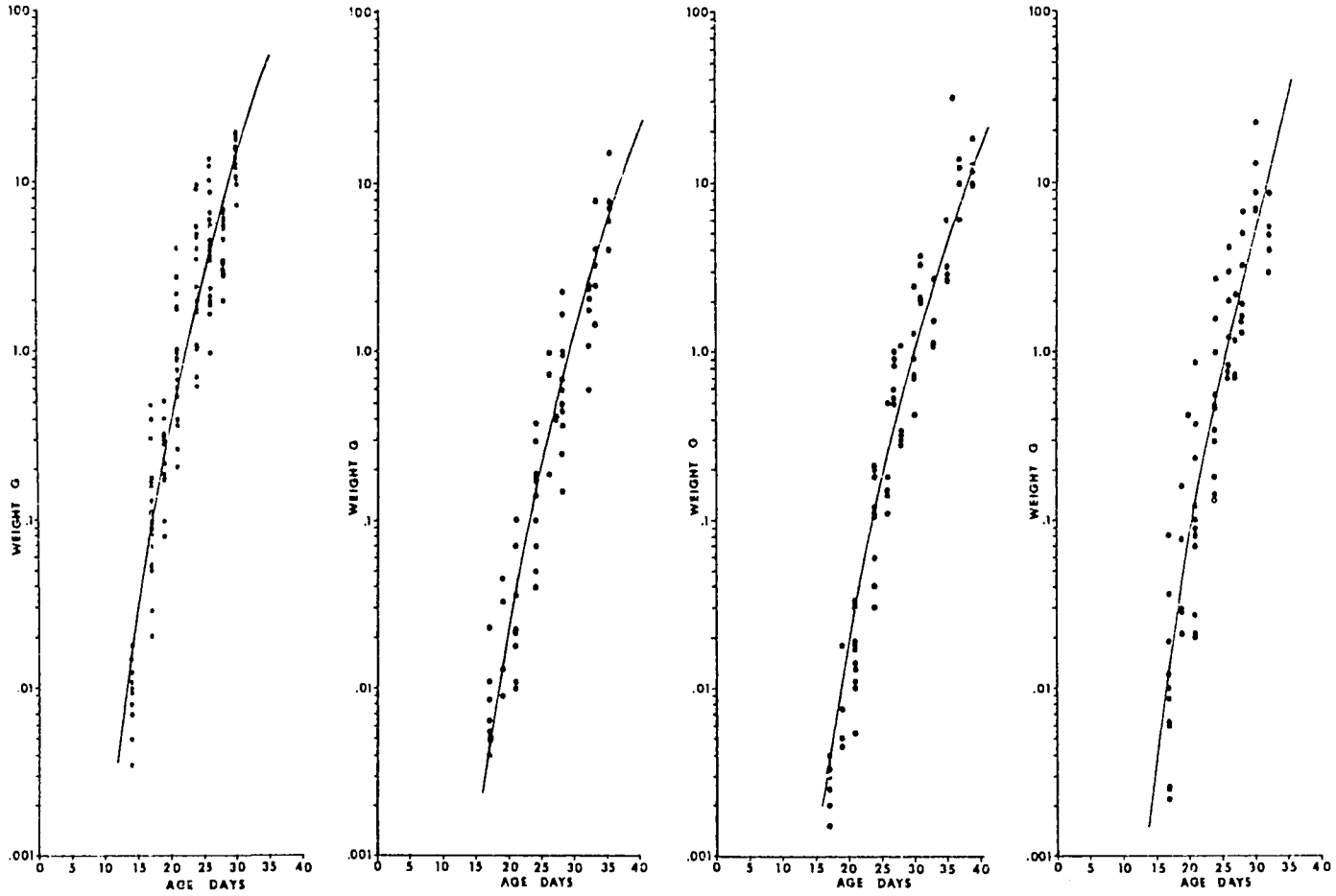

Figure 1. Growth of juvenile A. juliana on U. fasciata and U. reticulata from Kewalo and U. lactuca and U. reticulata from Sand Island.

Several estimates of juvenile growth in the field were obtained by following the growth of recently settled cohorts. The growth of these cohorts was superimposed on the growth curve obtained in the laboratory and is shown in Figure 2. The slopes appear to be very similar which suggests growth rates determined in the laboratory closely approximate those in the field at least for the juvenile stages. For purposes of calculations later the growth rates in the laboratory will be assumed to be the same for those in the field if the algal food is the same.

2) Growth of Adults in the Field. Animals which were kept in the cage at Sand Island grew to sizes a little larger than the average size outside the cage but still did not approach the sizes attained by animals in the laboratory. Figure 3 shows the growth of the two groups of animals raised in the cage. Early growth of the caged animals was rapid and comparable to some laboratory-obtained rates. Once the caged animals began to lay eggs, there was very little subsequent somatic growth. By contrast, there was no change in the growth rate of laboratory reared animals when egg laying commenced.

Early in the study the assumption was made that the monthly size distribution data would reveal some information on growth rates of A. juliana in the field, unfortunately this was not the case (see Figures 24-28, Chapter IV). There were two problems associated with analyzing such data. First, if growth in the natural field situation is similar to growth in the cage and growth of the released spotted animals, then monthly sampling was probably insufficiently frequent to discern growth rates. Animals raised in the laboratory grow for no

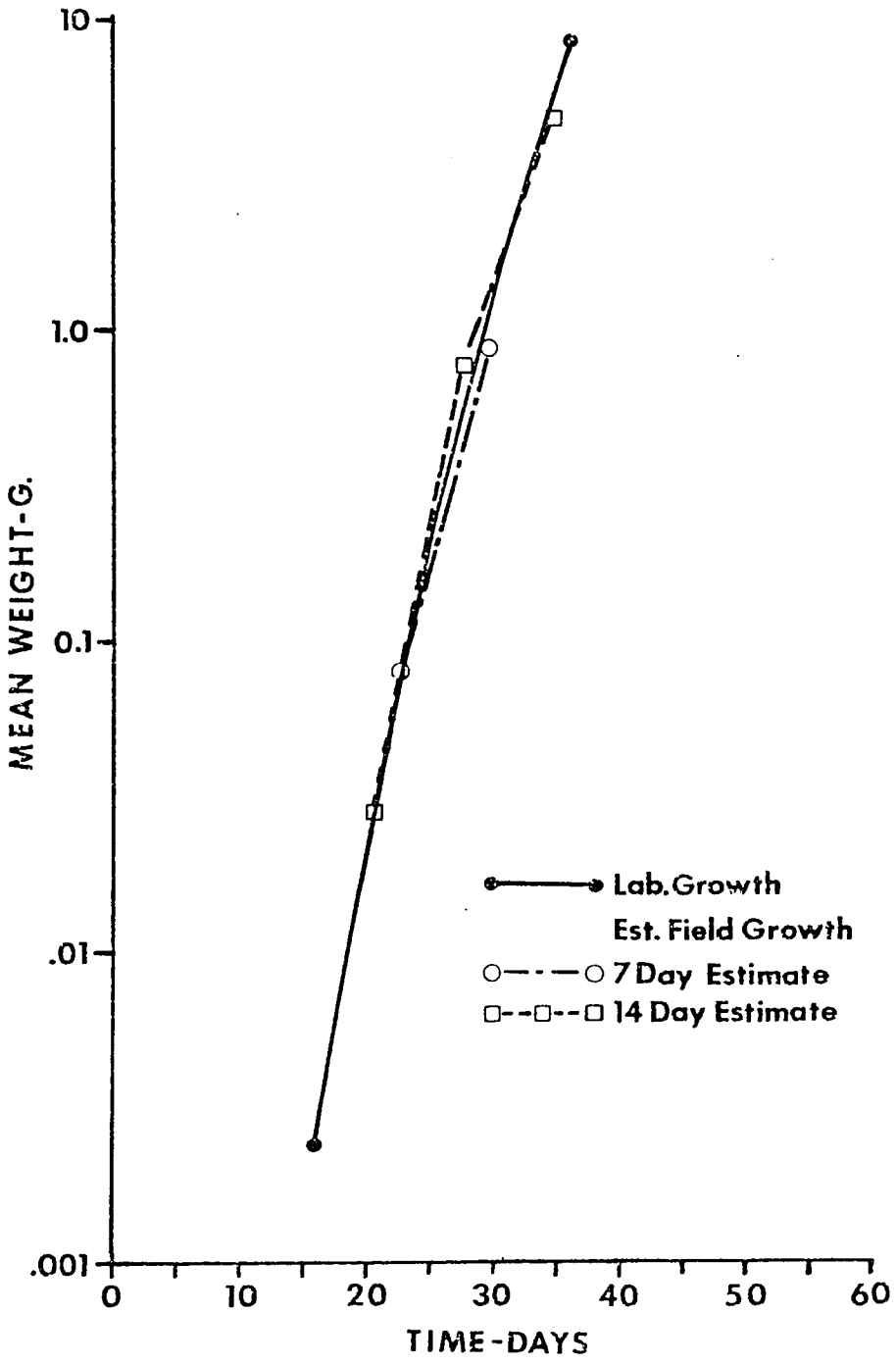

Figure 2. Estimated field growth of juvenile A. juliana compared to laboratory growth. Both fed on U. reticulata from Kewalo.

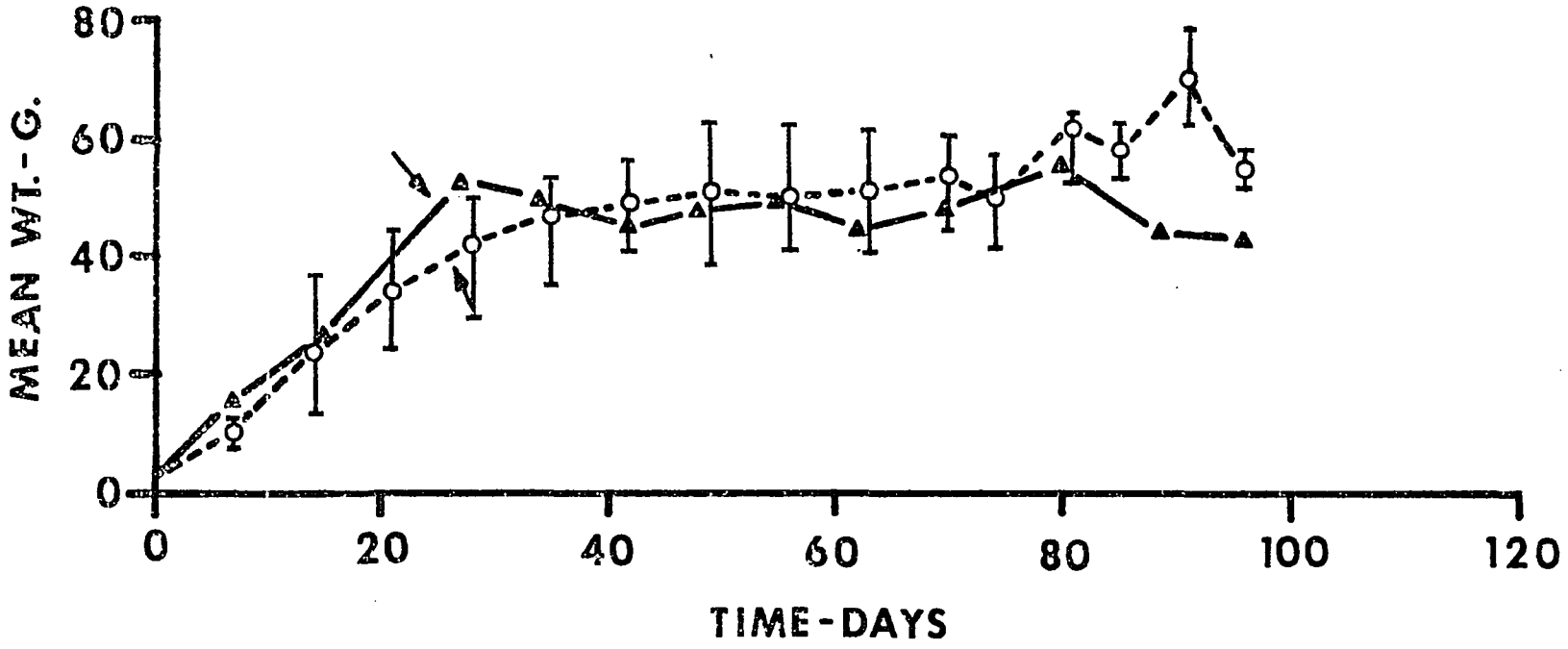

Figure 3. Growth of two groups (circles, N = 5; triangles, N = 4) of A. juliana raised in the cage at Sand Island. Arrows indicate first egg production. Bars indicate ranges.

more than two months and the caged animals attained their maximum size in four to eight weeks. The spotted animals released in the field stopped growing after one month.

Constant recruitment further complicated efforts to follow growth in field populations. In every case where the average or maximum size of a population was increasing the population density was also increasing. It was impossible to tell if all the animals were growing larger or if only the recently settled animals were responding to the more favorable habitat by growing to a larger size.

3) Tagging Experiments. The only direct data on field growth were from the spotted animals seeded into an area at Sand Island cleared of A. juliana. Figure 4 shows the growth and longevity of the spotted animals. Again, the animals showed rapid growth for the first two weeks which leveled off at about the time of sexual maturity.

4) Adult Growth in the Laboratory. Growth of A. juliana was very fast under ideal laboratory conditions. Animals would eat almost continuously provided they were shaded from direct sunlight and provided with adequate amounts of food and water flow. They would occasionally stop eating to copulate, lay eggs or "sleep". A. juliana will eat all three types of Ulva, but growth characteristics are different on each (see Figures 5, 6, and 7).

Laboratory grown animals can achieve sizes close to 300 g while animals found in the field rarely exceed 40 g (see Figures 24-28, Chapter IV). This disparity between laboratory and field growth is puzzling since there always seemed to be abundant food available, at least, at the Sand Island habitat.

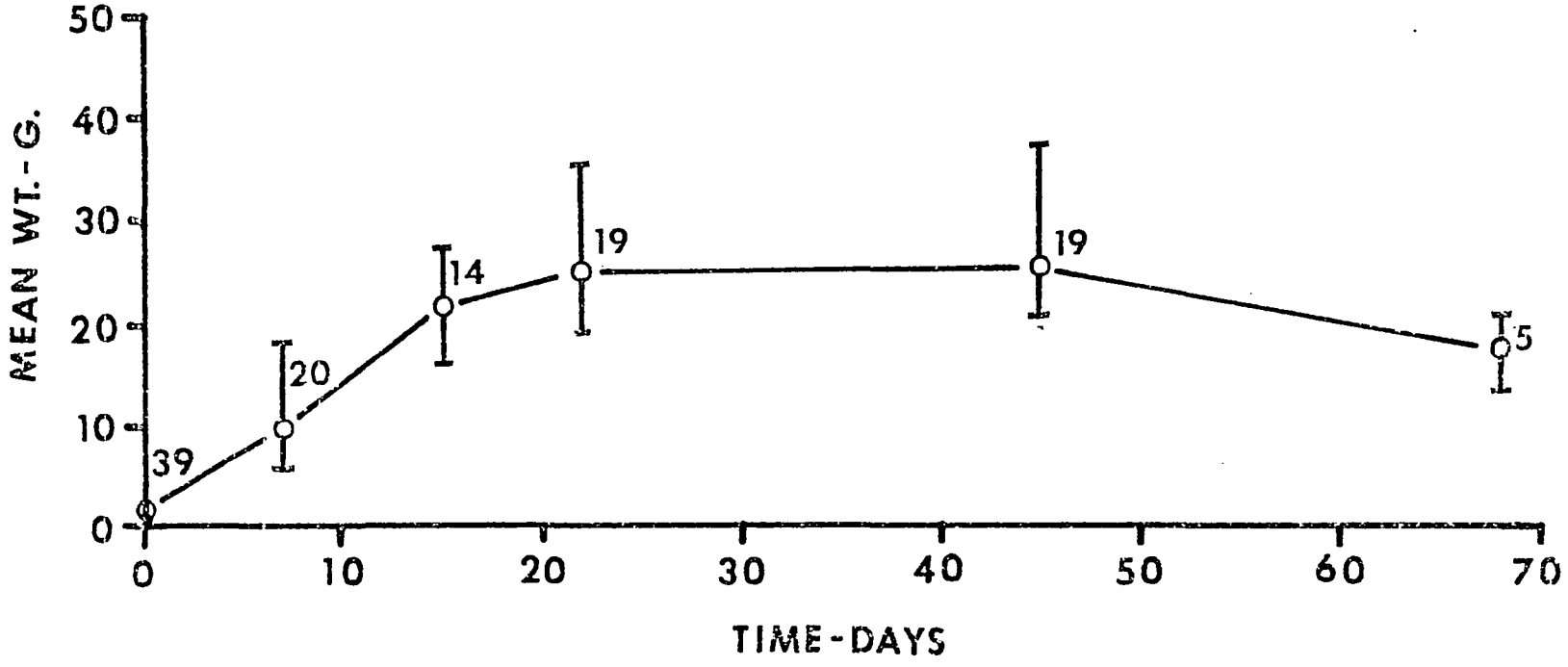

Figure 4. Growth and survival of a group of 39 spotted A. juliana released at Sand Island. Numbers indicate animals surviving. Bars indicate ranges of weights.

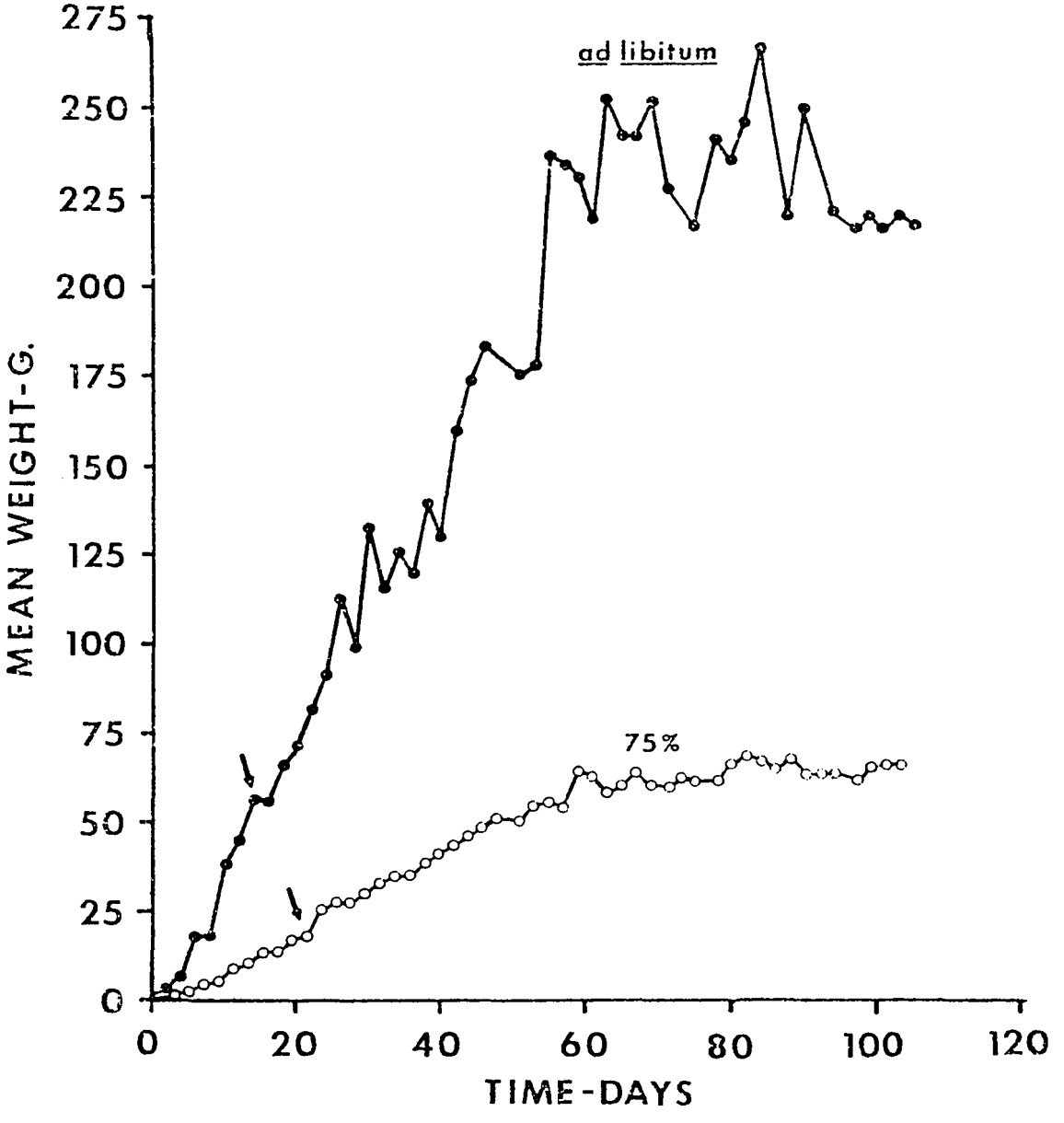

Figure 5. Growth of A. juliana fed ad libitum and at 75% of the ad libitum feeding rate. N = 5 in each group. Both fed U. lactuca. Ranges are shown in Table 9 (Appendix).

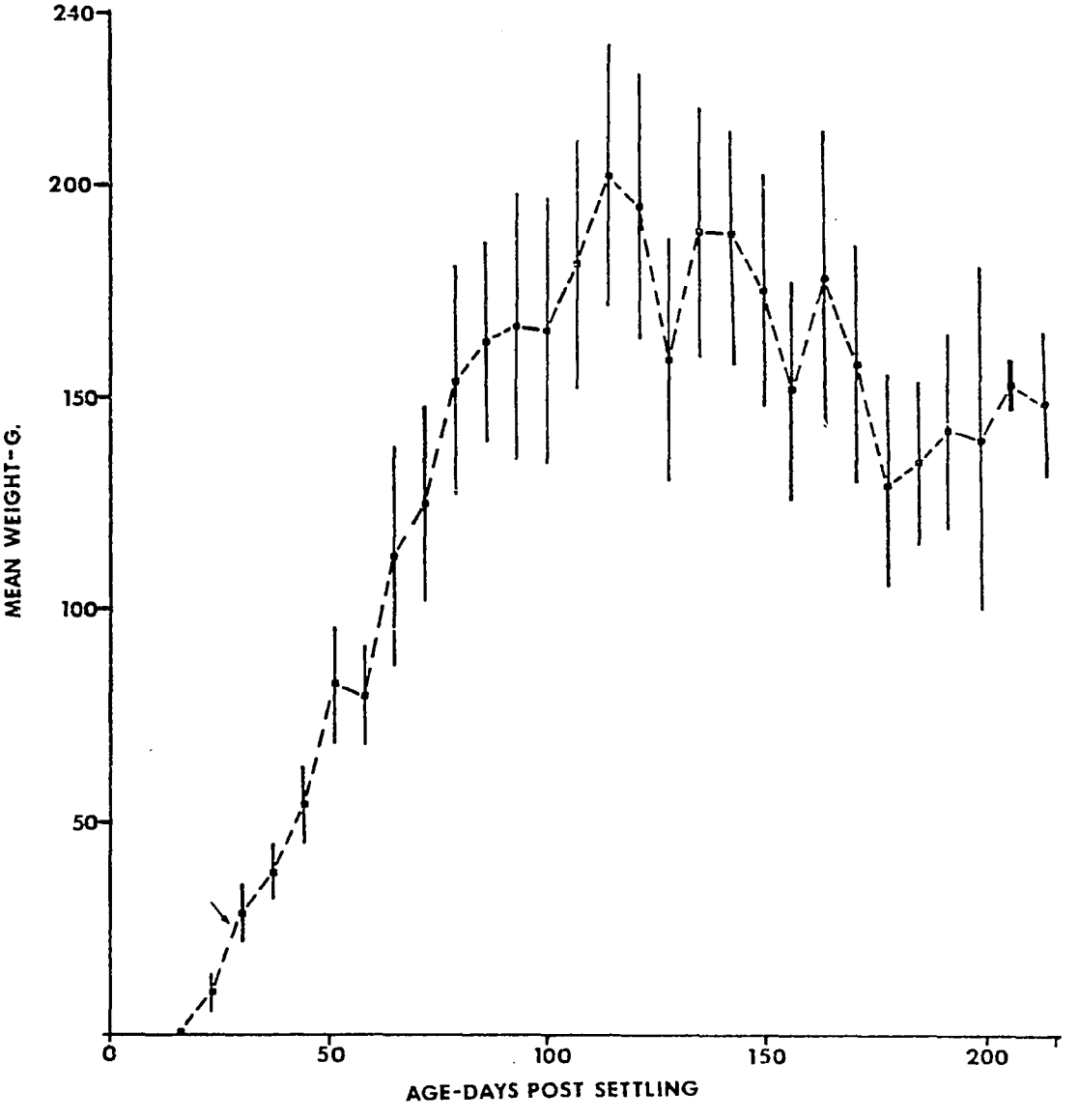

Figure 6. Growth of A. juliana fed ad libitum U. fasciata. N = 33 animals. Bars indicate one standard deviation on either side of the mean.

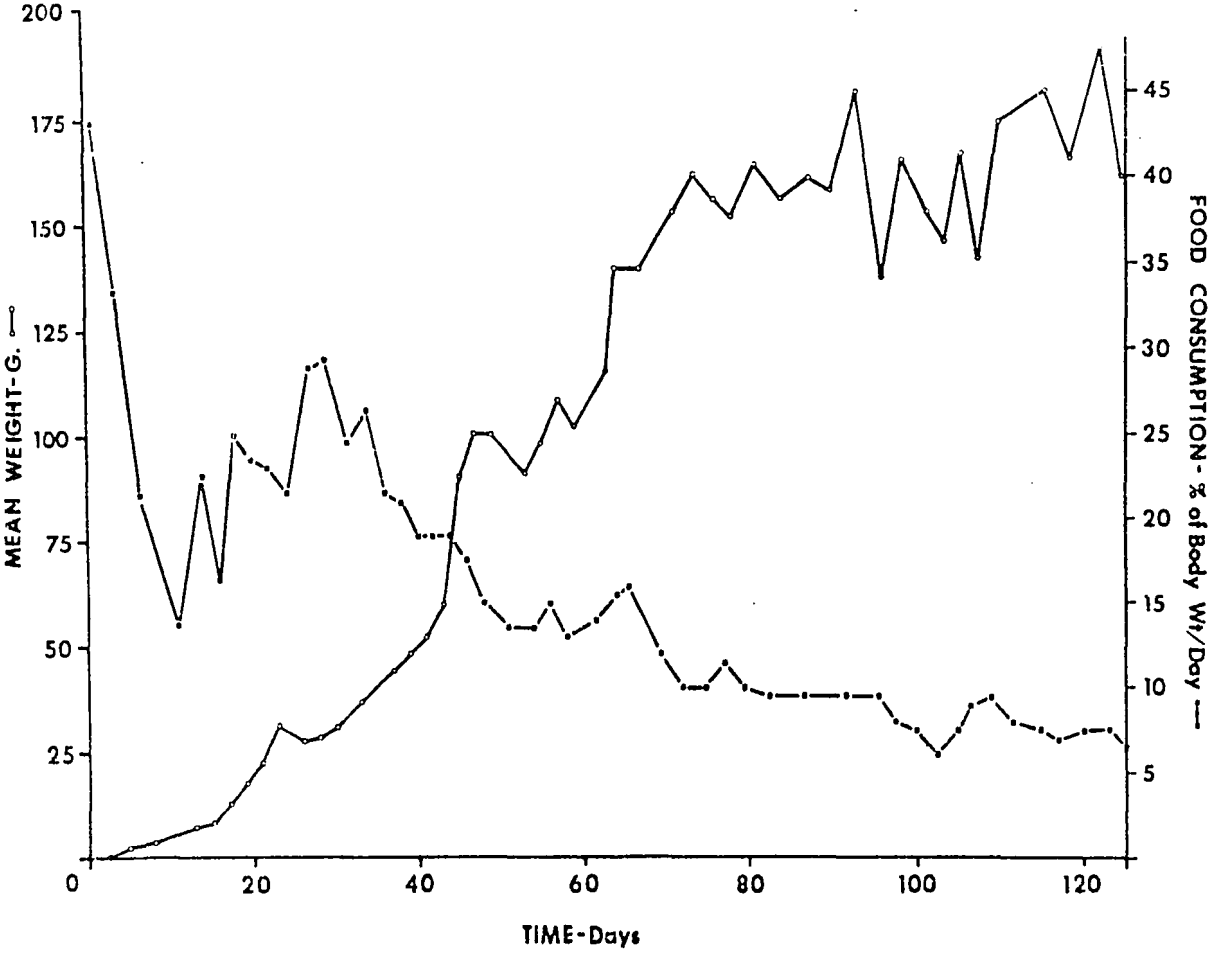

Figure 7. Growth and feeding rate of a pair of A. juliana feeding on U. reticulata, N = 2. Individual weights are shown in Table 10 (Appendix).

The differences between the sizes achieved in the laboratory and the field, and possibly between different habitats in the field, may be partially explained by the results of the following laboratory experiments.

5) Effects of Water Movement on Growth. Water movement had on the growth and maximum size of two groups of Aplysia (Figure 8). The animals in the tank without strong current grew faster from the start of the experiment and were often twice as large as those exposed to strong current. There was also a higher rate of mortality in the tank with strong current with over half the animals dying in the first 20 days of the experiment. The slugs in the control tank were often seen feeding while those in the tank with current were under rocks most of the time.

6) Effects of Light on Growth. Direct sunlight also had an inhibitory effect on the growth and maximum size of A. juliana. Figure 9 compares growth of animals subject to normal ambient light levels with those kept in darkness. Animals in the tank receiving ambient light spent all of the daylight hours buried in the gravel and fed only at night. Animals kept in the dark spent almost all their time feeding. It is interesting to note that the animals kept in the dark laid relatively fewer eggs.

7) Effects of Feeding Levels on Growth. The amount of food available to an animal will affect its growth rate. Indications were that animals in the field grew rapidly up to the point of sexual maturity and then stop growing. A set of experiments was conducted wherein animals were fed ad libitum until the start of egg laying and then were

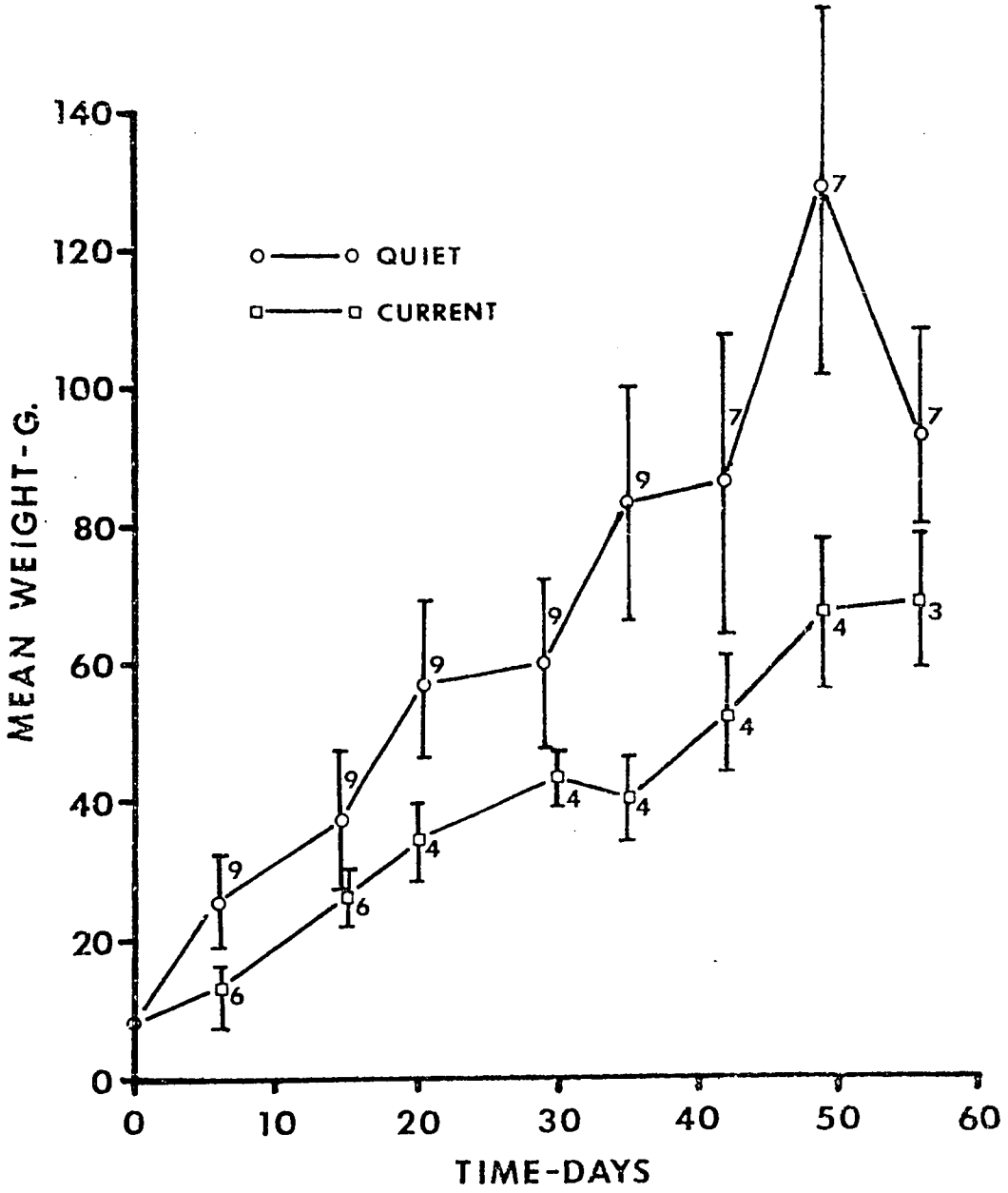

Figure 8. Growth and survival of A. juliana raised in tanks with and without current. Experiments began with 10 animals in each group. Numbers indicate animals surviving. Bars indicate one standard deviation on each side of the mean.

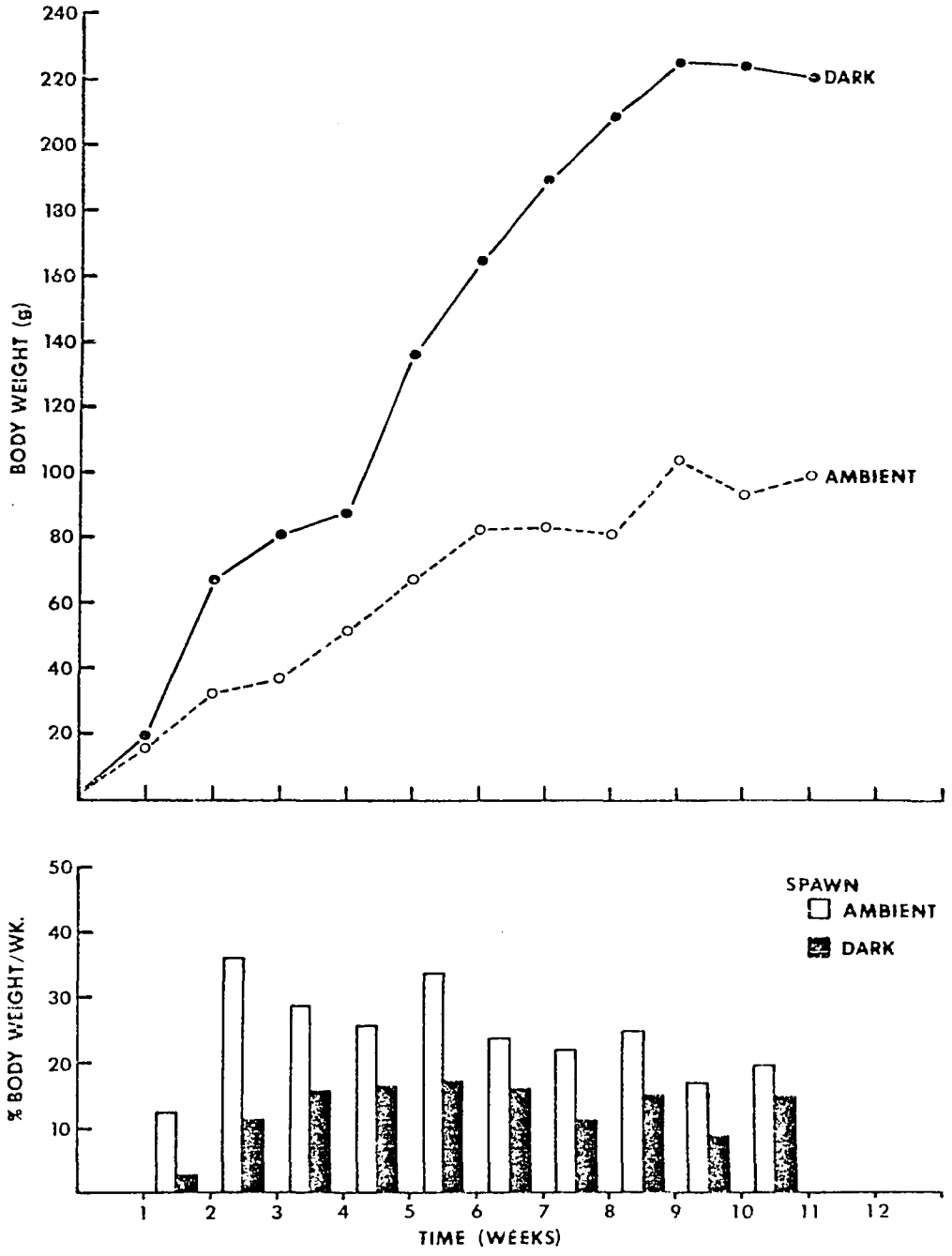

Figure 9. Growth and fecundity of A. juliana grown under ambient light and in darkness. N = 5 in each group. There was no overlap in ranges between the dark and ambient groups after 2 weeks.

put on various restricted feeding rations in an attempt to mimic growth seen in the field. Figure 10 shows the growth of three groups of animals which were fed constant but reduced amounts of food 10, 20, and 30 g of Ulva lactuca per animal per two days after the onset of sexual maturity. The amounts fed corresponded to 25, 50, and 75% of their body weight at the onset of sexual maturity (40 g) per two days. Each feeding ration had a characteristic maximum size and plateau weight. In all the experimental groups, the maximum weight was obtained on the same day even though the growth rates up to that point were different.

A second feeding experiment examined the effect of maintaining animals on a reduced diet beginning at a very small size (less than 2 g). These animals were fed 75% of the rate an ad libitum fed animal of the same age would have eaten. Figures 5 and 11 show how a 75% ration affected growth rate, maximum weight, and relative egg production. Sexual maturity was delayed for about one week in the rationed group. Growth of the rationed animals was, of course, slower, but it leveled off at the same time as in ad libitum feeding. Egg production was also lower for the rationed animals although the general shape of the production curve was the same (Figure 11).

In the third experiment animals were given a small but constant amount of food in an attempt to produce the small adult sizes seen in some of the poorer habitats. These animals were given only 1/2 g of Ulva per day and grew only to a little over 8 g. They reached sexual maturity at weights of about 6 g and, even on this small food ration, they laid an average of 5.25 g of eggs per individual lifetime (Figure 12). Although

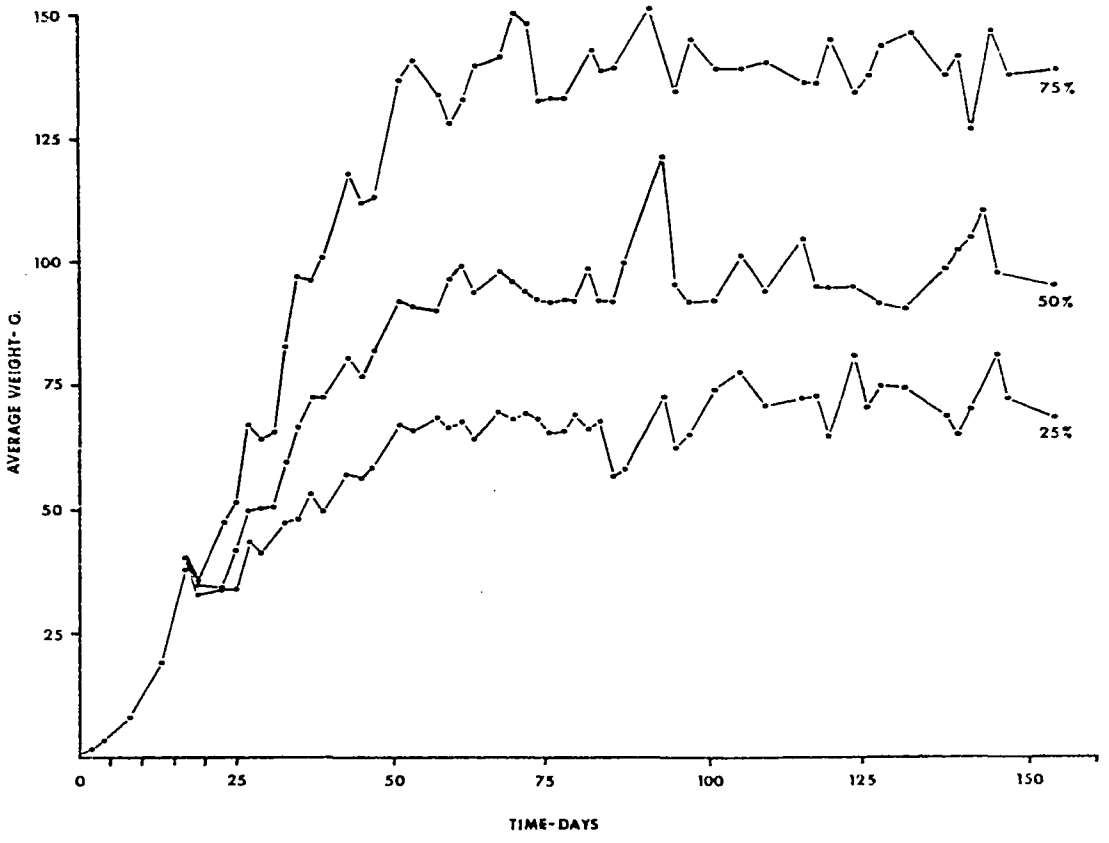

Figure 10. Growth of three groups of A. juliana fed different rations of U. lactuca. All were grown to 40 g under ad libitum conditions. Animals were then split into 3 groups of 4 each and fed 10, 20, and 30 g of Ulva per animal per 2 days. Standard deviations for these mean values are available in Table 8 (Appendix).

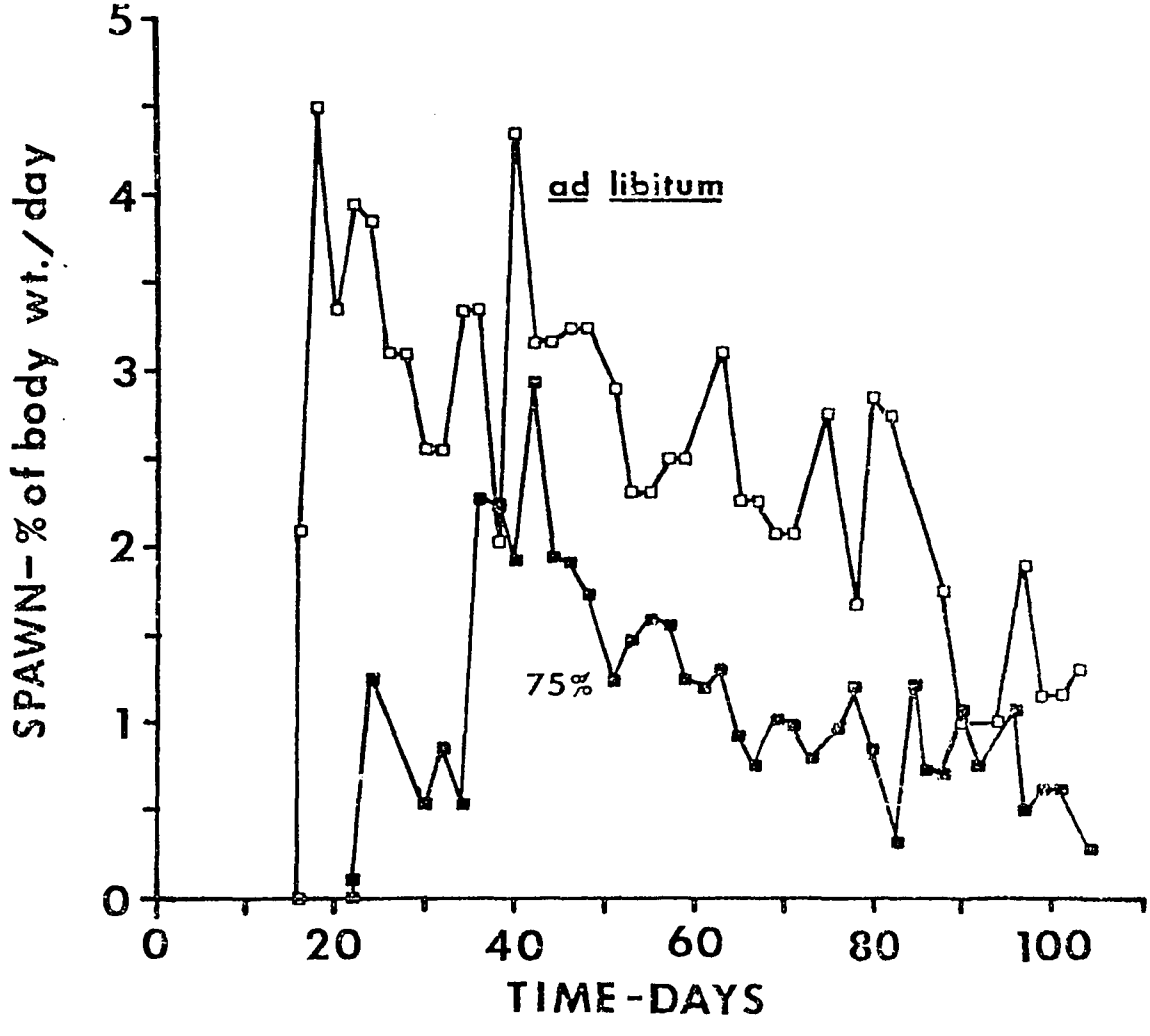

Figure 11. Relative egg production of A. juliana fed ad libitum and at 75% of the ad libitum feeding rate. N = 5 in each group. Both fed U. lactuca.

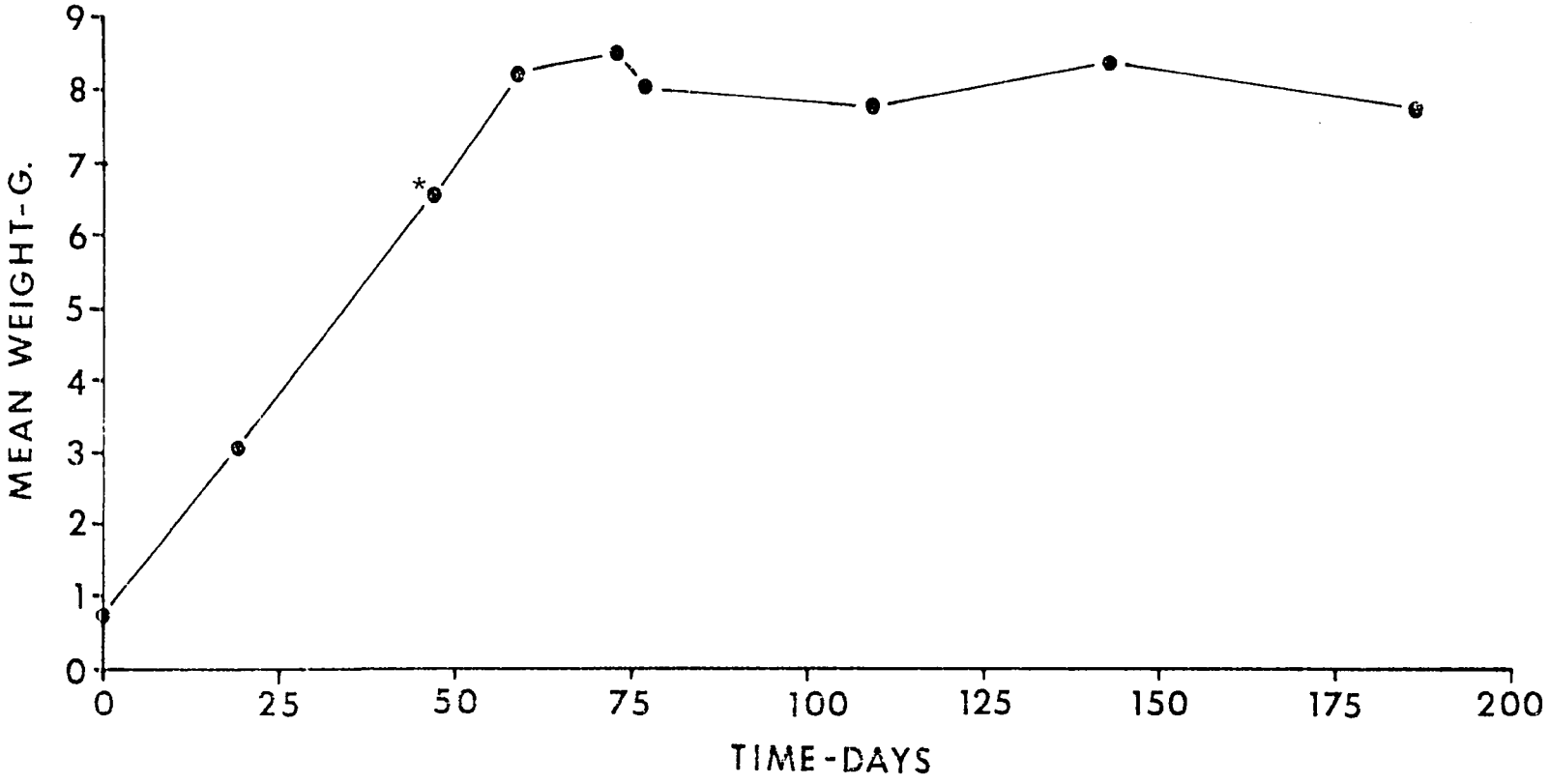

Figure 12. Growth of a pair of A. juliana fed .5 g of U. lactuca per animal per day. * indicates first egg production.

they attained only very small maximum sizes, their growth patterns were the same as those on other rations; i.e., they grew relatively rapidly for the first few weeks and then stopped growing at about 60 days.

The final growth experiment dealt with the question of whether growth rate was a function of age or size. Figure 13 compares the growth of three groups of animals: one was fed ad libitum throughout the experiment; one was starved for eight days at the beginning and then returned to ad libitum feeding; and the last was fed ad libitum until they weighed 40 g, then fed a small ration of 4 g per animal per two days for about seven weeks and then returned to ad libitum feeding. The results indicate that the rapid growth phase does not necessarily have to occur early in the life of A. juliana. The growth period of A. juliana seems to be limited in duration but not in placement. Growth can occur at different times in the life of the animal depending on food availability; it can even be broken into segments separated by periods of non-growth.

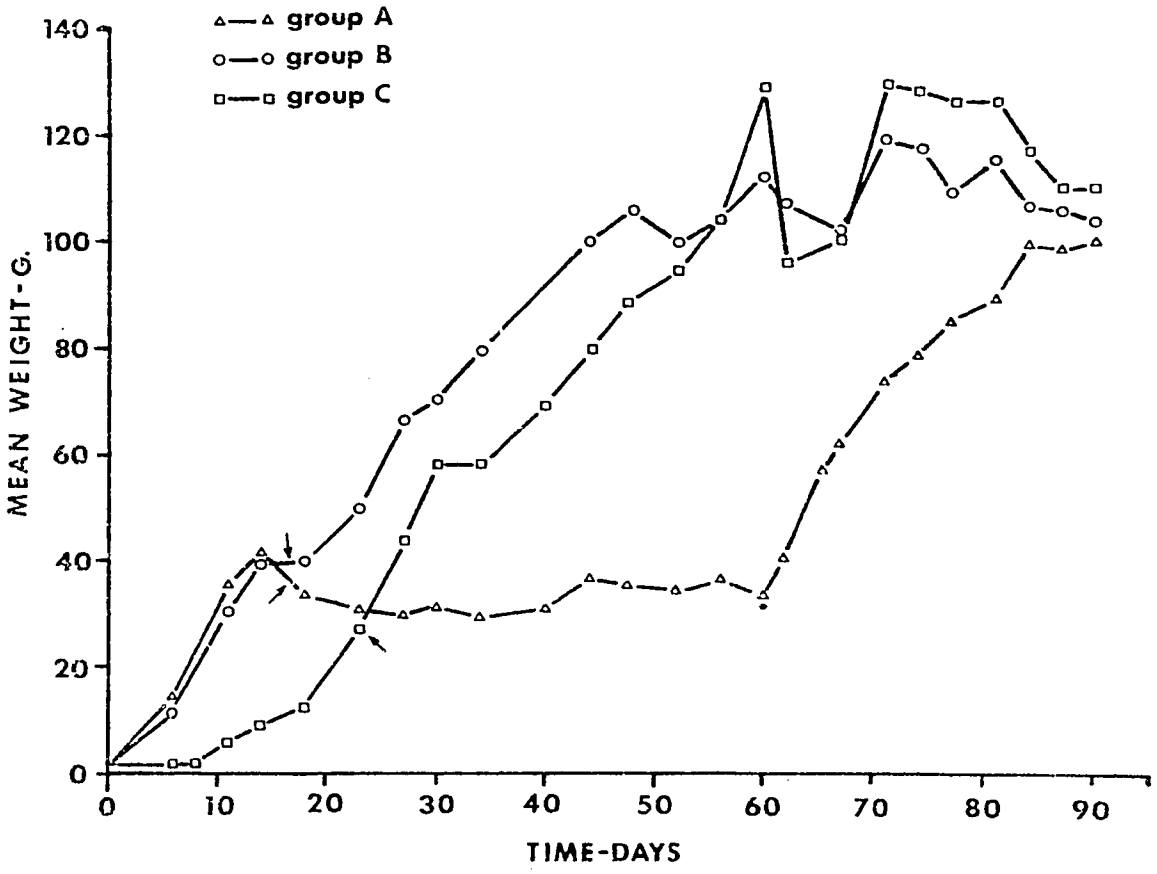

Figure 13. Growth of 3 groups of A. juliana under different feeding regimes. ○ = Fed ad libitum throughout. △ = Fed ad libitum to sexual maturity and then fed 4 g of U. lactuca per day per animal for 7 weeks and then returned to ad libitum (indicated by *). □ = Starved for 8 days and then returned to ad libitum. Arrows indicate first egg production. N = 4 in each group.

Discussion.

Von Bertalanffy (1960), defined growth as "the quantitative increase of a living system which results from the prevalence of anabolism of building materials over catabolism." But growth in an individual organism does not go on indefinitely and different animals grow at different rates, for varying amounts of time and achieve different sizes. Very little is known about factors determining when and how much an animal grows. Ultimately the size limit of an animal is determined genetically (von Bertalanffy 1960). Although a certain degree of variation exists between individuals, in general, there is a characteristic adult size for most species. Factors that can modify this genetic program include food, behavioral interactions and temperature. There are limits on how much these factors can effect the size of a specimen; one cannot grow a slug the size of a horse by feeding it well and lowering its temperature. Only so much genetic plasticity is available, but nevertheless this plasticity can still be significant to a species or population, especially when survivorship or fecundity is directly related to size.

Juvenile Growth

Animals experience their fastest growth rates when they are small. A. juliana grew extremely fast shortly after metamorphosis and increased its size from a 350 µm veliger to a 0.2 or 0.5 g juvenile in three weeks. At an age of two weeks they were doubling their weight every day. During this juvenile period they fed constantly and consumed more than twice their weight in Ulva each day. Growth during their juvenile period when they are living on the algae can be expressed mathematically using the power function $Y = AX^B$. The growth rate in the laboratory seems to

be a good approximation of growth rate in the field. Carefoot (1967a, 1967b, 1970) found that different algal foods resulted in different growth rates in species of Aplysia and similar differences were seen in the present study. Ulva fasciata promoted the fastest growth of A. juliana with U. lactuca, U. reticulata from Kewalo, and U. reticulata from Sand Island resulting in slower growth in that order. These differences in growth rates may be significant to natural populations since they determine how long the juveniles remain on the algae and are exposed to high mortality rates. Adult mortality rates are discussed in Chapter IV.

Adult Growth in the Laboratory.

A juliana are potentially rapidly growing, highly fecund animals capable of consuming large amounts of algae in a relatively brief lifetime. Laboratory growth studies showed that under ad libitum feeding conditions they grow to sizes well over 200 g and live for six to seven months. Even though there was a great deal of variation in the maximum size attained, the shapes of the growth curves were similar. The animals grew very fast for the first six to eight weeks, maintained a constant weight for three or four months, and lost weight as they began to senesce. This same type of growth curve was observed for A. kurodai in Japan (Nishiwaki, et al. 1975), A. juliana in Japan (Usuki, 1970), A. dactylomella, A. parvula, Dolabella auricularia and Stylocheilus longicauda in Hawaii (Switzer-Dunlap, in press).

There was variation in the maximum weights attained both in the experiments using different algal foods and between replicate experiments using U. lactuca as food. The differences in growth of animals fed

different foods (Figures 5, 6, 7) can be explained by variation in the nutritional value of the algae.

The differences in growth in the two experiments where U. lactuca was fed ad libitum (Figures 5 and 13) may be explained by differences in water temperature or differences in the nutritional quality of the algae, or both. Temperature is without doubt capable of causing changes in growth patterns. Animals maintained at cooler temperatures usually grow slower, reach larger sizes and live longer (Prosser 1955; Bullock, 1955). In Japan where the water temperature ranges from 8-27^{o} C, A. juliana has been reported to attain weights exceeding 450 g (Saito and Nakamura, 1961), and Switzer-Dunlap, et al. (in prep) report similar weight in animals grown at 20^{o} C. Sea water temperature in Hawaii varies only about four degrees annually (23-27^{o}). The two U. lactuca feeding experiments resulting in animals with mean maximum sizes of 130 and 267 g were run when water temperatures were 25 to 26^{o} and 23 to 24^{o} respectively. The effects of temperature on growth thus may have caused some of the differences observed in maximum sizes.

Variation in the nutritional quality of the algae might also contribute to the differences in maximum sizes observed in the ad libitum feeding experiments. Paine and Vadas (1969) reported seasonal variations in the caloric content of several species of algae and Medcalf, et al. (1975), Mohsen, et al. (1974a, 1974b, 1974c) and Mohsen, et al. (1972a, 1972b) all reported various biochemical changes occurring in species of Ulva at different times of the year or with different experimental treatments. Qualitatively, the algae at Kewalo, and especially Sand Island, changed a great deal throughout the year. At times, more often

in the summer and late fall, the algae were very light in color, thin and slimy, and in general not as "healthy" looking as they were at other times. This change applied to all the species of algae found at any one place. The algae at Sand Island also changed in caloric content during the year with higher values occurring in the late fall and winter months (see Figure 23, Chapter V).

Raw sewage from Honolulu is pumped into the ocean off the shore at Sand Island. Usually the offshore trade winds blow the sewage out to sea and probably little of the nutrients reach the shore. But when there are southerly winds, much of this "enriched" water is blown ashore. Field work at such times varied from unpleasant to impossible. This nutritional source may explain why the Ulva crop at Sand Island was much more persistant and dense than it was at many of the other locations around Oahu. On two occasions southerly winds occurred when the algae were very thin and light in color. In both cases the winds persisted for several days and within three or four days the algae had changed to a very dark green and were thick and robust in appearance.

Adult Growth in the Field.

Individual A. juliana found in natural habitats are never as large as those grown in the laboratory (see Figures 24-28). Laboratory "giants" have also been reported in Phyllaplysia taylori (Beeman 1970), Stylocheilus longicauda (Switzer-Dunlap, et al. in prep.), and Octopus maya (Van Heukelem, 1976). However growth is not always limited by environmental conditions. Van Heukelem (1976) reported growth to be the same for Octopus cyanea in the field and reared in the laboratory with ad libitum feeding.

There are many factors that can influence the maximum sizes attained by animals in the field. (1) Size dependent mortality results in lower maximum and mean sizes of animals in a population, but is probably not the case with A. juliana as no predators of large animals are reported or were seen. Aplysia juliana probably escapes most of its predators by growing to larger sizes. (2) Growth can, in some cases, be regulated by behavioral mechanisms. In animals which are territorial or have social orders, food can be unevenly distributed and this leads in turn to non-normal size distributions. Aplysia are not territorial and tend to show aggregating behavior which could result in depletion of algae near the animals. (3) Temperature, as discussed earlier, can affect the growth characteristics of animals. Animals at all field locations visited in this study as well as animals used in laboratory experiments grew to larger sizes in the colder winter months. (4) The most likely factor to affect growth and possibly explain the differences between maximum sizes of A. juliana in the field and laboratory is the availability of food. The effect of reducing food rations either from early in the juvenile stage (Figure 5) or from the time of sexual maturity (Figure 10) was to reduce the maximum size attained. In the field situation the animals would not always have an overabundance of food. Changes in food density have been reported to affect the growth and maximum sizes of animals in field populations of Thais (Spight, 1974), Acmea scabra (Sutherland, 1972), Navanax inermis (Paine, 1969), Lymnea sp. (Hunter, 1975), Phyllaplysia taylori (Beeman, 1970), and Aplysia punctata (Carefoot, 1967c).

The physical factors light and water movement also indirectly affect access to food. Ebert (1968) has suggested that in urchins, access to food may be more important to growth than the abundance of food. This appears to be the case in A. juliana. Their nocturnal/diurnal activity pattern reduces the amount of time they spend feeding and thus reduces their ability to grow. The effects of water movement on growth probably also function by reducing feeding time. The rapid growth observed in most laboratory experiments was possible only as long as the animals could have constant access to algae. Water movement and direct sunlight, led to slower growth and resulted in smaller maximum sizes. Animals in the field cage were always supplied with excess food and still did not approach the sizes attained in the laboratory; they did, however, get larger than those outside the cage. Caged animals supplied with ad libitum food grew larger than the animals outside the cage which suggests that even though there appears to be abundant food in the habitat, growth is still food limited. A pair of animals might deplete the algae in their immediate area which could reduce their access to food. In addition, the largest A. juliana found in the field occurred when the Ulva was densest. The reduced growth in the field is probably the result of the combined effects of food abundance and factors that limit the access of animals to that food.

Short periods of starvation or limited food do not affect the potential for growth in A. juliana. Animals which were starved for eight days or maintained on such low rations that they stopped growing for eight weeks, still achieved the same final weight as the controls if they were eventually returned to ad libitum feeding. Chia (1971)

observed the same phenomenon in the saccoglossan Olea hansineensis. While growth rate has been long known to be primarily a function of size rather than age (von Bertalanffy, 1960), there is a limit to how long the growth period may be delayed. Reduced rations will usually increase life span within limits (McCance and Widdowson, 1974). While an animal's aging process may be slowed down by insufficient food for growth, it cannot be stopped, and the inevitable process of aging will eventually eliminate the potential for growth. But, after eight weeks on maintenance rations, which is one-third of the maximum life-span, A. juliana could still resume rapid growth. The mechanisms controlling when and how much an animal may grow are poorly understood. Since these animals can at any time respond to increased food by growing, then animals in the field must be food limited throughout their life and their small sizes must not be a result of being stunted from poor feeding early in life.

Aplysia juliana probably do have a limited amount of time in which they can grow, but it does not have to be in the early part of their life nor does it have to be continuous. Rather, the period of growth can be broken up into what Parker and Larkin (1959) called "growth stanzas". The ability of an animal to grow and thus increase its fecundity whenever food is available, be it early or late in life, has distinct selective advantage.

The effect of longer life and slower growth at low temperatures along with the ability of animals to grow in response to an increase in food at any time may help to explain the persistance of short lived, seasonal nudibranchs and may apply to other marine animals as well.

These nudibranchs which have a life span of supposedly only a few months usually appear in the summer (Miller, 1962; Clark, 1975; Swennen, 1961). Where these species reside for the rest of the year has been somewhat a mystery; it is highly unlikely that their larval period would last many months. One possible explanation is that many of these populations survive by recruitment from non-seasonal populations elsewhere (Clark, 1975). Another is that there are very small populations existing in deep water or scattered throughout the range of the species that survive the winter and produce the offspring that become the larger, more obvious summer populations, or summer populations produce a cohort of larvae that settles in the late fall or early winter when the water is very cold and there is very little food available, both of which would tend to extend the life span. These animals would be very small and inconspicuous. In the spring when the temperature climbs and food becomes more abundant the animals would begin to grow. Beeman (1970) and Usuki (1970) reported overwintering populations of opisthobranchs which grew little or not at all. None of the ideas discussed above is mutually exclusive and some fit certain species better than others. The effects of temperature and size-related growth on life span may play an important role in the survival of subannual species.

CHAPTER III

Recruitment

Introduction.

A population, to remain in existence for more than one generation, must recruit new members to replace those lost to mortality and emmigration. Recruitment can occur through reproduction and immigration. Here, considering only recruitment accomplished through larval settlement, we will deal with two specific problems, the timing and the rate of recruitment.

The timing of recruitment can be very critical to a population or species. There are many selective pressures which could influence the timing of reproduction and recruitment. Seasonal variations in the availability of settling substrate, food supply, predation pressure, temperature, mortality rates and probably many other parameters can affect the timing of reproduction and recruitment in marine animals. The timing of reproductive periodicity can be as precise as a few hours or as long as many months. Similarly, many species have characteristic seasonal periods of recruitment. While seasonality in recruitment in more tropical areas is not so evident as that in temperate habitats, it does exist and seasonal peaks are common. A great deal can be learned about the selective pressures acting on a species if one can discover which environmental factors its reproductive and settling activities are keyed to.

The rate of recruitment in relation to population size is valuable but very difficult information to obtain. The magnitude of this ratio is important in determining mortality rates of any population.

Whether these rates vary between seasons, years or locations may have a great effect on the stability of their populations. Changes in adult population size and food supply can affect its fecundity which in turn may or may not affect recruitment rates. The relationship between population size, fecundity, and recruitment rates is very important in assessing the stability of any species or population.

To work with recruitment and mortality rates one must decide when an animal is regarded as a recruit and when it has become a member of the adult population. It seems reasonable to define a recruit as an animal that has either just hatched from a direct developmental mode or one that has just settled and metamorphosed from an indirect mode. However, limitations in sampling techniques often influence the operational definition of a recruit. Newly settled marine invertebrates are very small and usually impossible to sample quantitatively in the field. Animals such as barnacles which settle on hard substrate and remain there permanently allow study from the point of settlement (Crisp and Barnes 1954, Weiss 1948, Connell 1961, Seed 1969, Hines 1977). Sampling recruits of nonsessile organisms is much more difficult. Usually figures for recruitment rates are derived from samples where "recruits" are already months or more old. (Frank 1964, Underwood 1975). Often highest rates of post-larval mortality for marine animals occur in the early period just after settling (MacGinite 1934). If one is interested in relative recruitment rates between years, populations, or habitats, it matters little at what stage recruitment is assessed as long as consistency is maintained. But if one is concerned with actual rates of recruitment or survival

of recruits, one must be very careful in sampling as well as interpretation.

There are several problems involved with attempting to directly assess recruitment in Aplysia. First, recruitment occurs not on the substratum but on algae, which varies in density over time. Algal density must be monitored and expressed as a function of area. Secondly, the very small (350 μm) recruiting Aplysia can be reliably counted only after about two weeks of growth by which time many of them may have died. Removing them from sources of mortality in the field by bringing them into the laboratory allows them the necessary time to grow; their ages and numbers at the time of collection can then be extrapolated. Finally, since there is probably a high rate of mortality in the early stages in the field, the extrapolations must include mortality adjustments. This was done by constructing a survivorship curve for animals on each algal species and field location.

Methods.

A. juliana larvae will settle on several species of green algae including Ulva fasciata, U. lactuca, and U. reticulata, all of which grow on Oahu. Very small juveniles can be found on all three species of Ulva in the field. U. reticulata and U. fasciata grow in the Kewalo Channel adjacent to the Kewalo Marine Laboratory, and U. reticulata and U. lactuca can be found at Sand Island. Recruitment of larval A. juliana onto these algal substrata was monitored at the main study site at Sand Island for both U. reticulata and U. lactuca and also U. reticulata at Kewalo.

Weekly samples of U. reticulata and U. lactuca were collected from Sand Island and U. reticulata from Kewalo. The fresh samples were placed in a mesh bag and spun 20 times in an overhead circle to remove excess water. An 800 g sample of U. reticulata and a 600 g sample of U. lactuca were weighed and placed into outdoor tanks of running, Cuno-Filtered seawater. Samples of U. lactuca were smaller because the algae could be maintained better at lower concentrations and examination of this species for juveniles was much more time consuming. The Cuno Filter with a pore size of 5 μm excluded additional recruitment of A. juliana larvae through the seawater system.

Since most of the aplysias were too small to see when the algae were collected, the algal samples were held for a period of time so the juvenile animals could grow to visible dimensions. Samples of U. reticulata were held for two weeks. U. lactuca proved to be much more fragile, did not last as long in the tanks, and was thus only allowed to stand for one week. At the end of the holding period, the algae were carefully inspected and the juvenile Aplysia removed and weighed. An age-weight relationship was determined by laboratory growth studies (Figure 1, Chapter II). These ages were then converted to ages at the time of collection by subtracting the amount of time the alga was kept in the holding tanks (14 days for U. reticulata and 7 days for U. lactuca).

Because the juvenile Aplysias live on the algae for about three weeks under field conditions, those larvae which have settled in day one could appear in more than one weekly sample. To determine how many

of the recruits had settled in the seven days prior to the day of collection, it was necessary to remove from a given count those animals which had settled in the two weeks prior to the one being considered. For example, consider a sample group of animals that might have been found on a weekly collection of U. reticulata from Kewalo which has been held for two weeks: 2 animals at .003 g, 3 at .009 g, 4 at .04 g and 5 at .30 g. From the age-weight studies discussed in Chapter II (Figure 1), it can be determined that animals .003 g are 16 days old (days post settling), .009 g are 18 days old, .04 g are 21 days old and .30 g are 25 days old. Subtracting 14 days from these figures gives their ages at the time of collection: 2 animals 2 days old; 3 animals 4 days old; 4 animals 7 days old; and 5 animals 11 days old. The 11-day-old animals would not be considered since they did not settle on the 7 days prior to the day of collection. The sum of the week's recruitment would be 2+3+4=9. Unfortunately, these figures as they stand are an underestimate of recruitment since animals are exposed to potentially high mortality rates every day and the algae were sampled only every 7 days. It was therefore necessary to calculate how many larvae actually settled on days 1-7 instead of simply how many were left at the end of a week. In order to do this it was necessary to establish daily mortality rates.

Daily mortality rates for the period when the juveniles were on the algae were obtained by summing the age-frequency data for animals on each algal type from all the weekly samples. One cannot use age-frequency data from a single week or even a month since recruitment occurs in random pulses. A single large pulse of settlement for a few

days could lead to a heavy overestimate of survival for those classes. But, if one considers all of the data collected over a very long time, one should be able to construct a survivorship curve with the effects of the pulse peaks being averaged out because a pulse has an equal probability of showing up in any of the age classes. The age-frequency data for 18 months were summed for juveniles on each algal species and the resulting numbers were fit to a curve which represents survivorship. These curves represent only averaged figures and any seasonal change in mortality is not seen. Knowing the number of juveniles in any given age group, one can extrapolate from the mortality curve the number alive at day one. The sum of these seven days of recruitment represents the weekly recruitment.

As stated above, the figure for weekly recruitment is based on 800 g of U. reticulata or 600 g of U. lactuca. However, it was also useful to express recruitment as a rate per unit area. Density of Ulva varied throughout the year at Sand Island requiring monthly assessment. Standing crop of Ulva was assessed by throwing a 1/2 square meter quadrat haphazardly about the study site and removing all the algae within it. Six samples were taken per month and carried to the laboratory where they were rinsed, separated by species, and dried to a constant weight at 60^{o} C. This weight could then be converted to the wet weight used on the recruitment studies. Knowing the weight of Ulva species per square meter and the number of recruits per 100 g of algae, one can calculate the number of new recruits per square meter per week.

Results.

Juvenile Survival.

All the recruits found on any one alga during the 18 months of the study were sorted by their estimated ages, summed and plotted by frequency. Figures 14, 15, and 16 show the frequency of finding an animal of any particular age on each of the three types of algae. The distribution of these frequencies produces survivorship curves for animals on each of the algal types. Smaller animals in age classes 1 and 2 for the U. reticulata data from Kewalo, classes 1 through 6 for U. reticulata from Sand Island, and in classes 8 through 14 for U. lactuca from Sand Island (classes 1 through 7 would not show up since this alga was only held for one week). The values for these days were not used in the construction of the survivorship curves. The data for each algal type were fit to several relevant curves (curve program on the HP 2000 computer). The relationship $Y = A + B\ (\ln(X))$ resulted in the best fit for data from U. reticulata from Kewalo and U. lactuca from Sand Island with R^2 values of .917 and .920 respectively. The relationship $Y = A^{(B \cdot X)}$ gave the best fit for the data from the Sand Island U. reticulata with an R^2 value of 1 .917. In these equations Y = age, B = slope, X = weight, and A = y intercept. The fit curves were then drawn through the age-frequency data for each algal type in Figures 14, 15, and 16. A total of 1,134 juveniles from the U. reticulata from Sand Island, 492 from U. lactuca from Sand Island and 3,978 from the U. reticulata from Kewalo were used to construct the survivorship curve for each of the algal types.

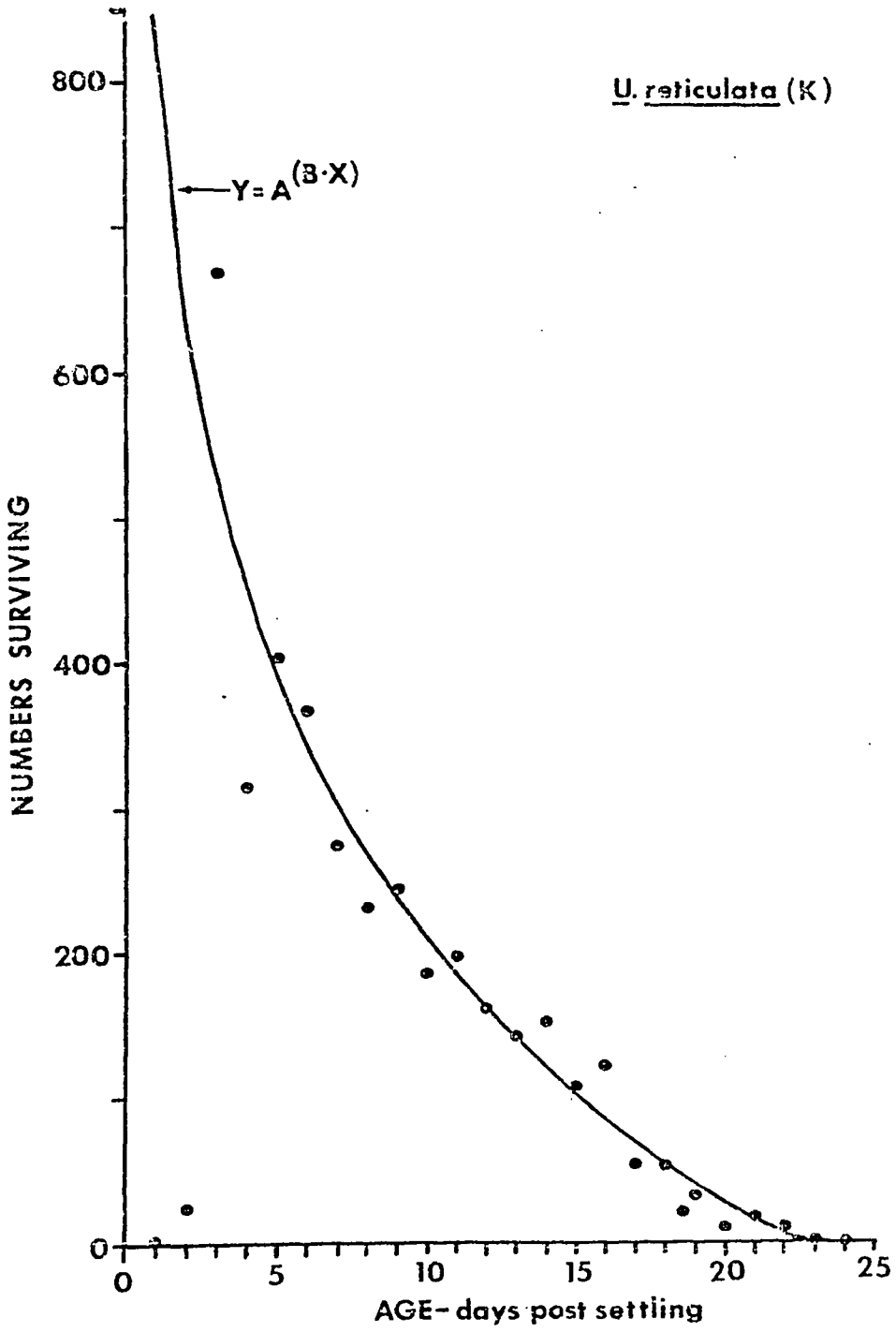

Figure 14. Size-frequency distribution of A. juliana recruits found on U. reticulata from Kewalo. N = 3978. Computer-fit curve is drawn through all but days 1 and 2.

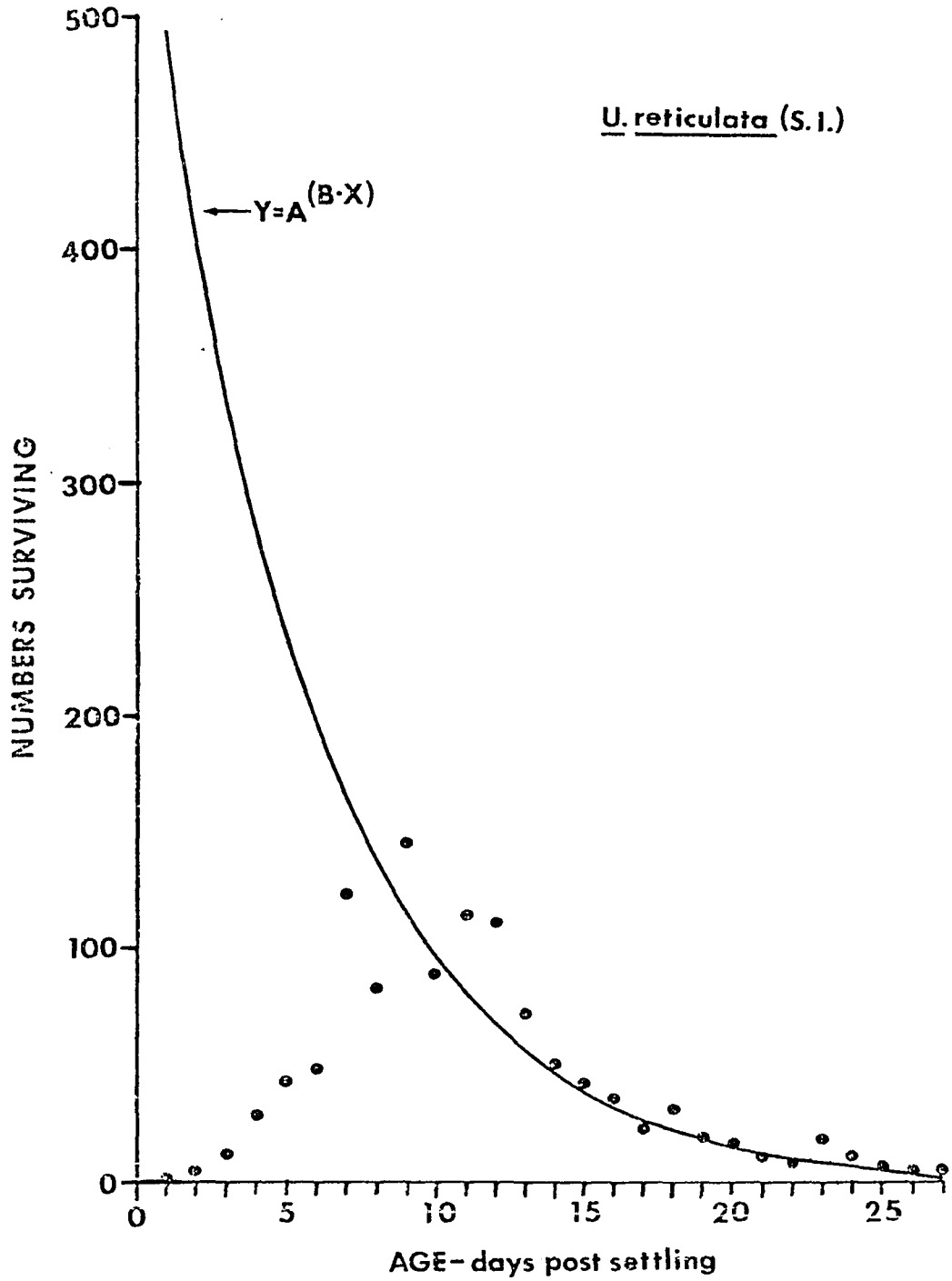

Figure 15. Size-frequency distribution of A. juliana recruits found on U. reticulata from Sand Island. N = 1134. Computer-fit curve is drawn through all but days 1-6.

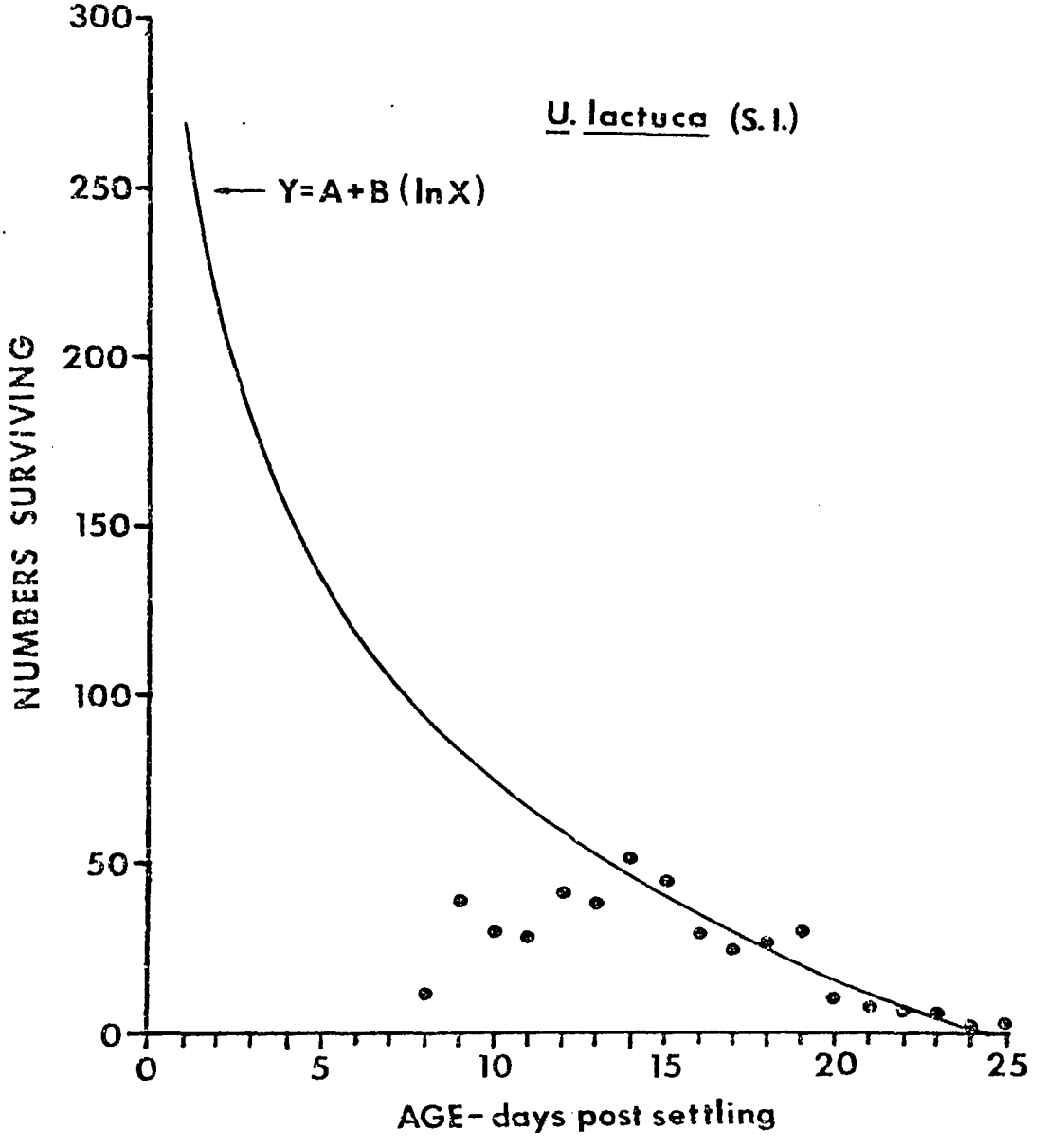

Figure 16. Size-frequency distribution of A. juliana recruits found on U. lactuca from Sand Island. N = 492. Computer-fit curve is drawn through all but days 8-11.

The frequencies predicted by these curves represent survivorship of the juveniles on the various algae. These extrapolated survivorship curves were also expressed as percentages surviving in Figures 17, 18, and 19 with the Y intercept values representing 100%. Expression of survivorship in a semi-log plot allows comparison of mortality rates between different ages and data of other investigators (Figure 20). Juveniles on U. reticulata from Sand Island showed constant mortality rate of about 16.5% per day while mortality on the other two algal types was higher early and late in the juvenile period. The high rates of mortality after day 20 were probably exaggerated due to the fact that the juveniles would have been leaving the algae for the adult habitat at about that age.

The survivorship curves (Figures 17, 18, 19) allow one to extrapolate from the number of animals alive on any particular day back to the number that were alive on the day that they settled (day 1). For example, using the figures for survival on U. reticulata from Kewalo, if on day 7 of a selected week, 50 animals were counted and the survivorship curve indicates that this corresponds to 37.3% of the number that actually settled on day 1, then the multiplication factor for day 7 is 2.68 (i.e. 100/37.3) and the number of animals that had originally settled out and represented by the day 7 count was 134 (i.e. 2.68 x 50).

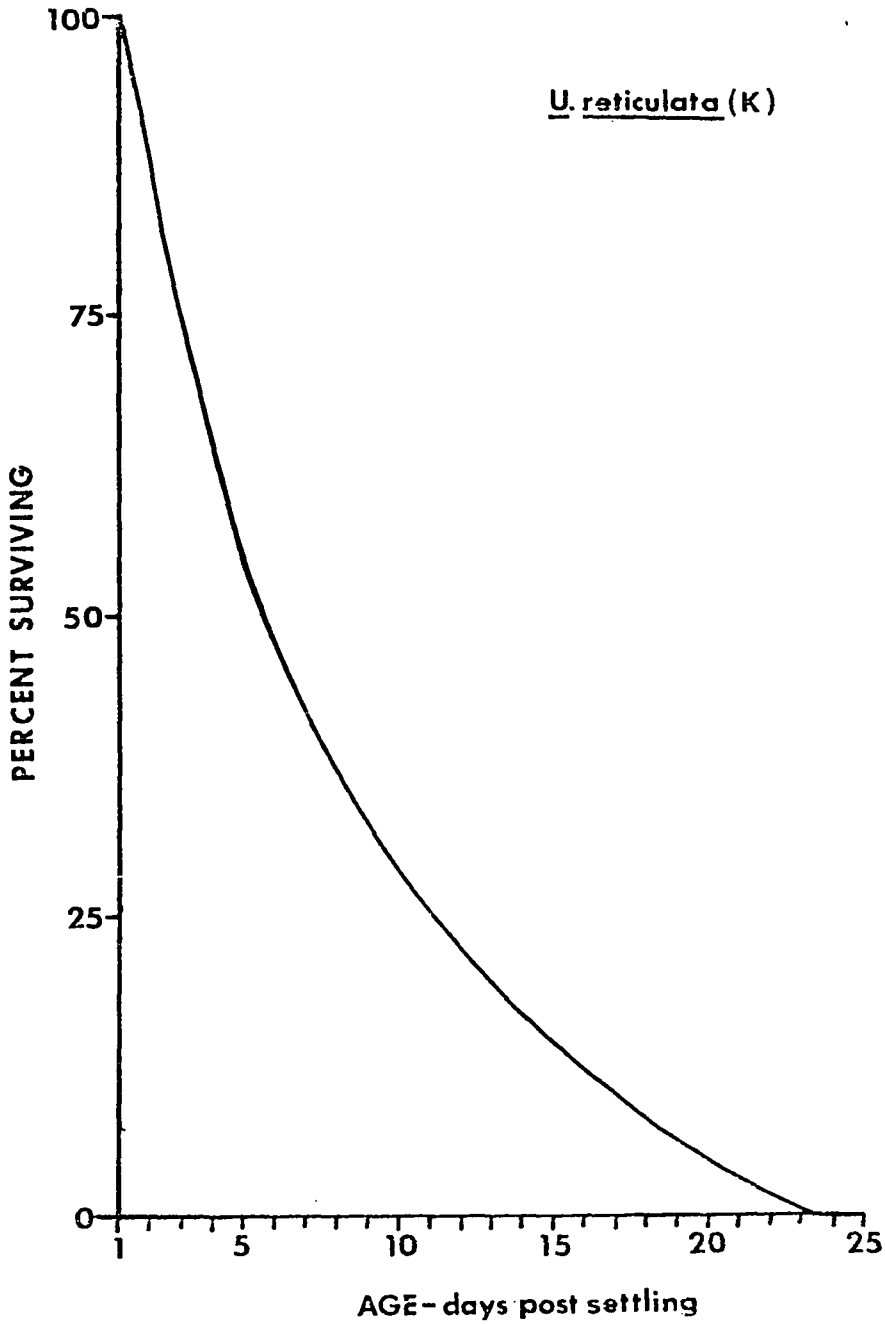

Figure 17. Daily percent survivorship of juvenile A. juliana on U. reticulata from Kewalo.

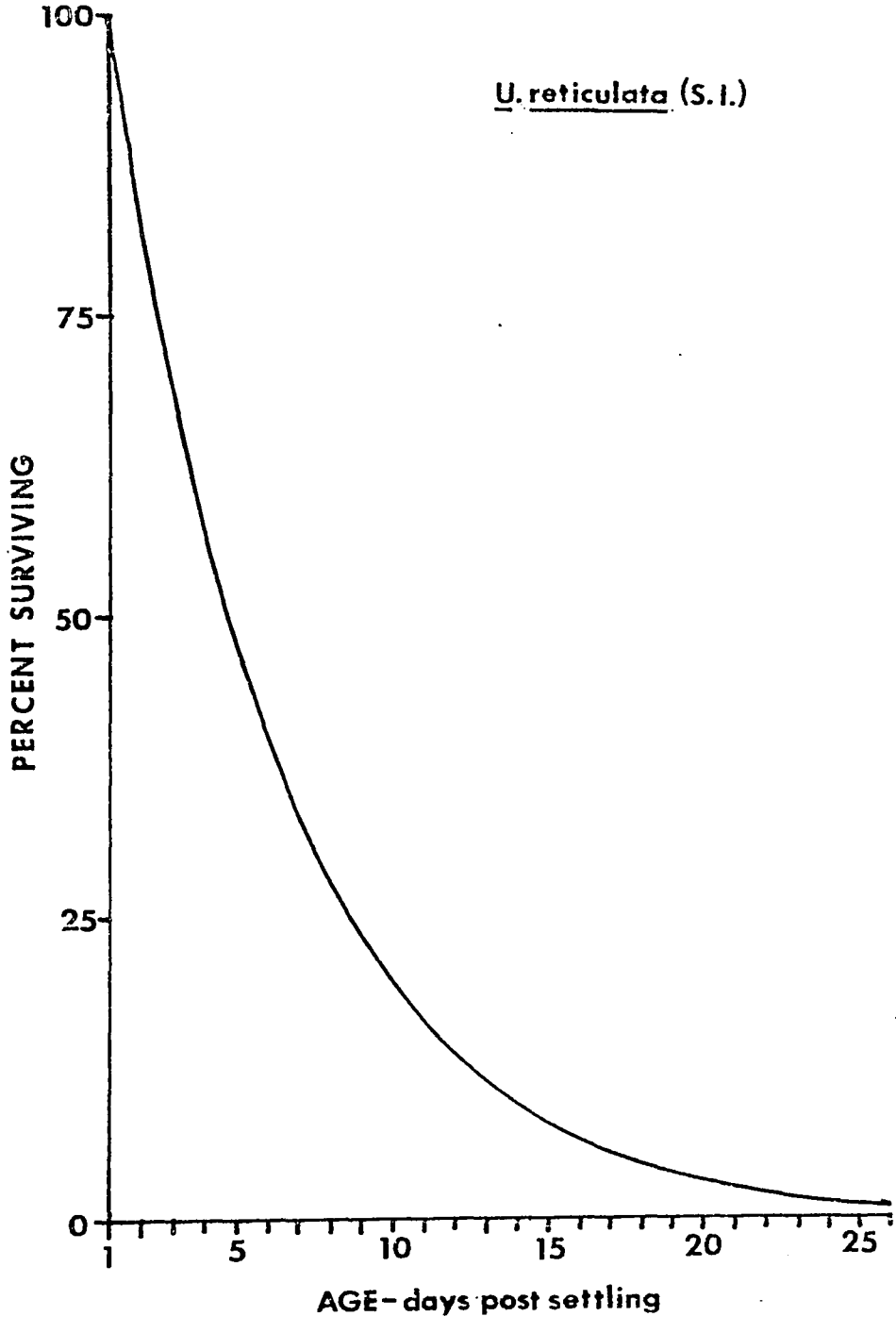

Figure 18. Daily percent survivorship of juvenile A. juliana on U. reticulata from Sand Island.

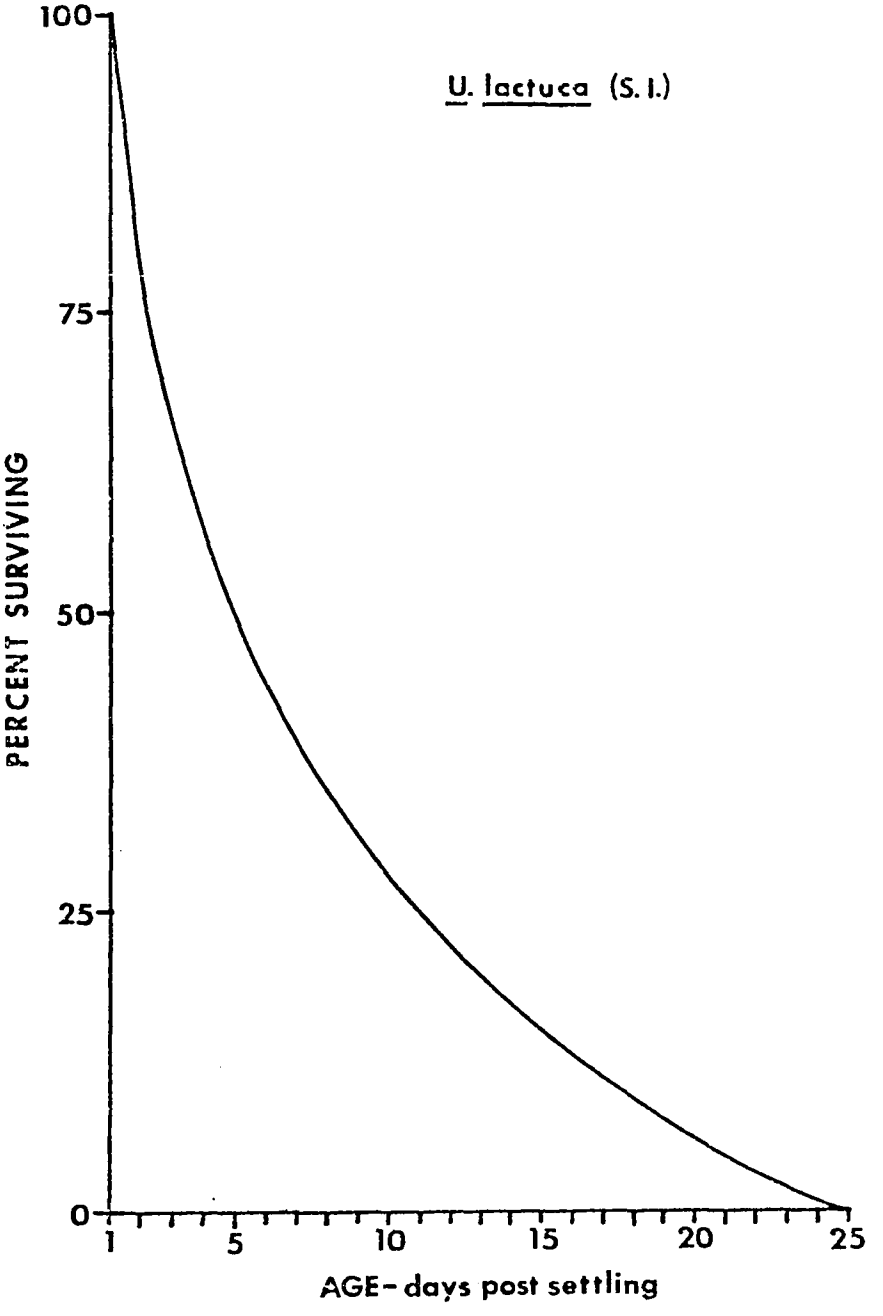

Figure 19. Daily percent survivorship of juvenile A. juliana on U. lactuca from Sand Island.

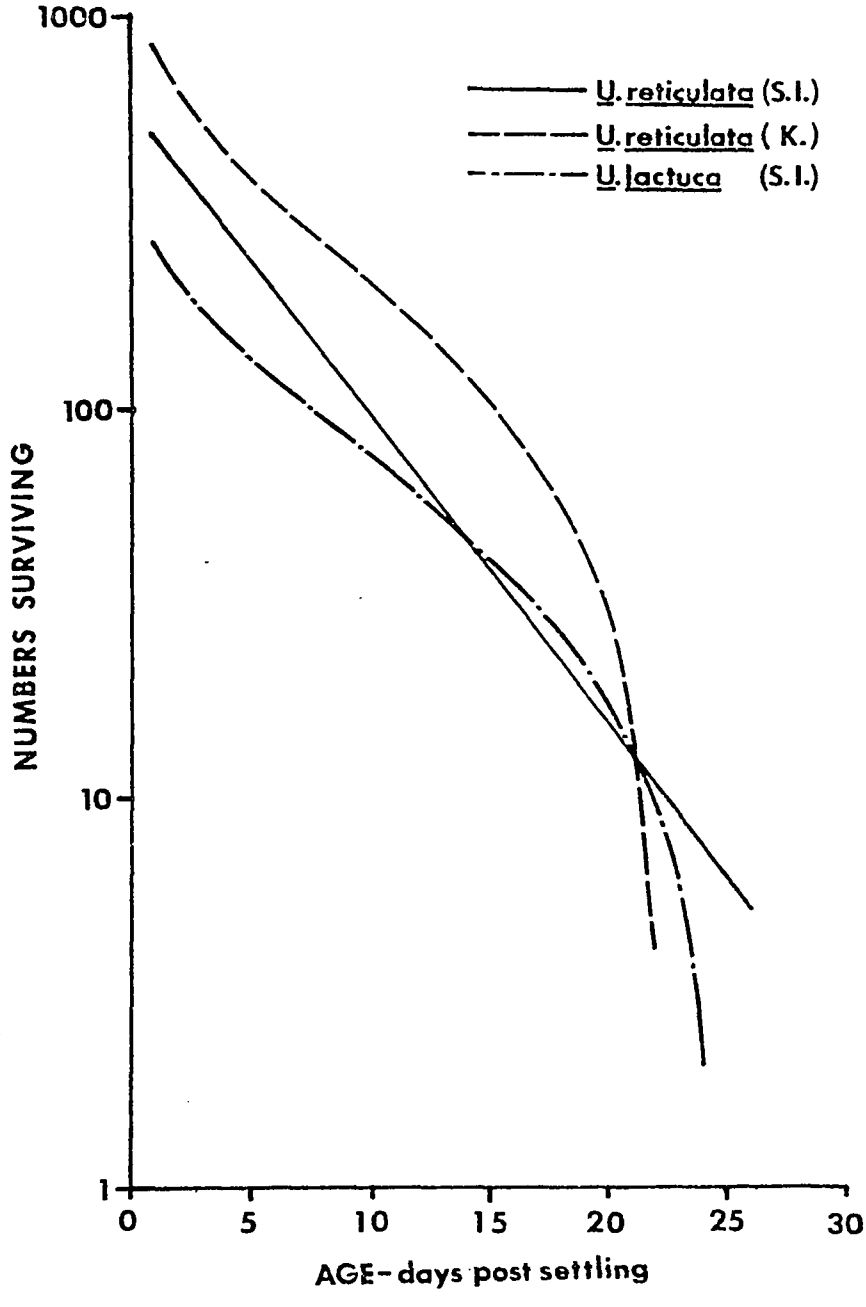

Figure 20. Survivorship of juveniles on U. reticulata and U. lactuca from Sand Island and U. reticulata from Kewalo.

Recruitment Rates.

Using the methods described above, the number of recruits per 100 g of algae that settled on any day for each of the three algal types was calculated. The data for each alga were lumped in seven day increments for weekly recruitment figures. The seven day increments that were used in these computations were days 3 through 9 for U. reticulata from Kewalo, days 7 through 13 for U. reticulata from Sand Island, and days 14 through 20 for U. lactuca from Sand Island since the data for the earlier days in each instance were underrepresented in the sampling. The underrepresentation of recruitment numbers for days 1 and 2 in the samples was probably due to the small sizes of the juveniles and the difficulty in finding them. The low figures for days 3 through 5 for the U. reticulata from Sand Island and days 8 through 13 for the U. lactuca was puzzling since the techniques for collecting and holding the algae were all the same. The algae from Sand Island never survived as well in the holding tanks as did that from Kewalo and the decaying alga was possibly toxic to the small animals whose corpses would not have been detected. Smaller animals were always more sensitive to poor water quality.

Weekly recruitment per 100 g of U. reticulata from Kewalo is shown in Figure 21 and reveals seasonality in settlement. Settlement was much lower in the summer and spring. There was also a large difference in settlement between years. In general, recruitment rates for U. reticulata at Sand Island show the same seasonal patterns as those at Kewalo Channel although the pulses did not always correspond and the rates were not as high as at Kewalo (Figure 21).

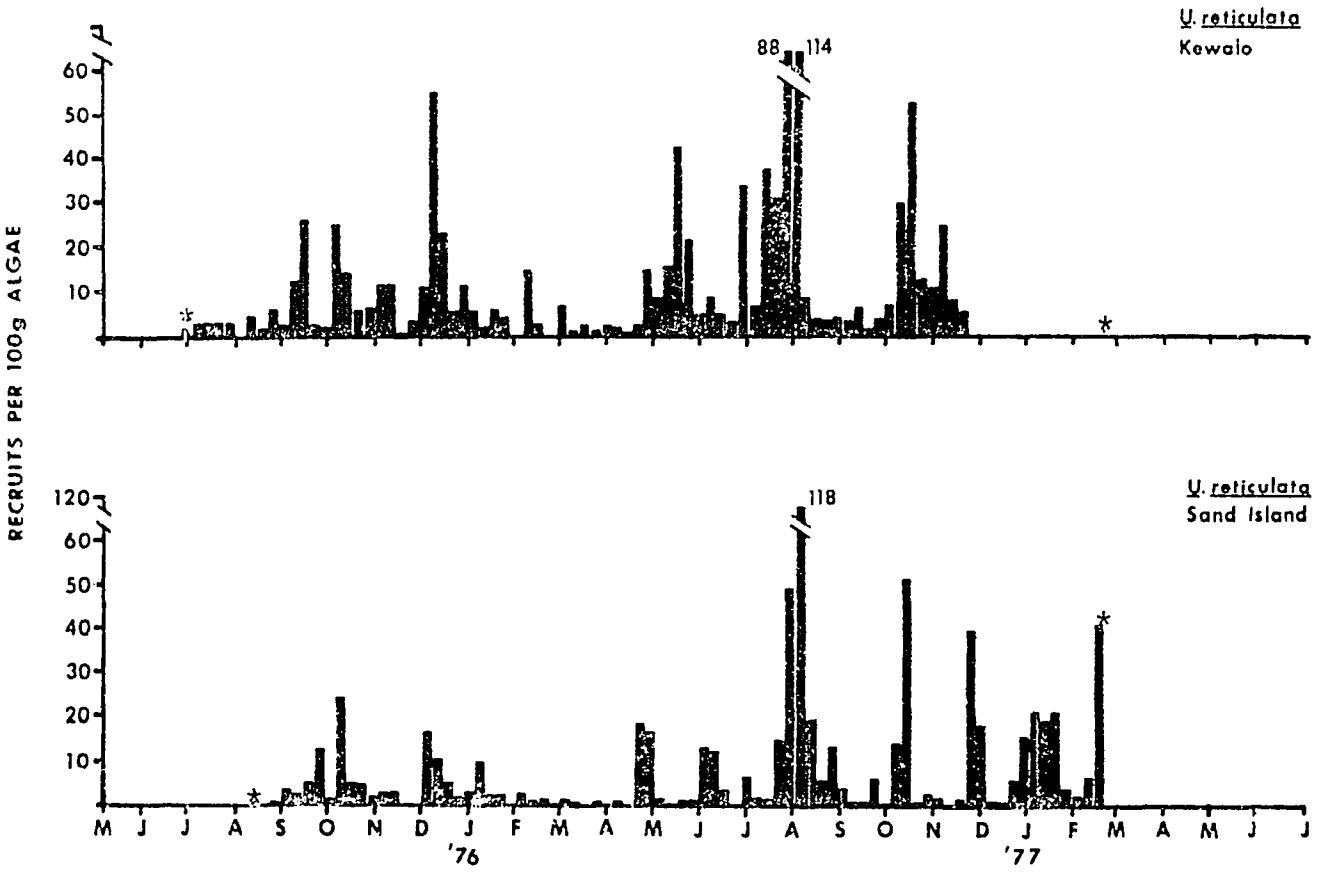

Figure 21. Recruitment rates per 100 g of wet U. reticulata at Sand Island and Kewalo Channel. Asterisks indicate times of first and last sampling.

For many considerations it was more useful to express recruitment as a function of bottom area rather than by weight of algal substrate. In order to do this it was necessary to relate the recruitment rate per 100 g of algae to the density of the Ulva crop. Standing crop of Ulva was not measured for the Kewalo area but did fluctuate in the course of the study. In February of 1977 Ulva completely disappeared from the Kewalo Channel site and has not reestablished itself since (to November 1977). Ulva crops at Black Point and other locations on Oahu were also observed to undergo similar fluctuations. The changes in algal density at Sand Island are shown in Figure 22. Both U. reticulata and U. lactuca followed the same yearly cycle of being very low in the summer and highest in mid-winter. With these figures and those for recruitment rates per 100 g of algae for the two algal species, total recruitment per meter square was calculated for the Sand Island study site (Figure 22). The same seasonality seen in recruitment expressed as a function of 100 g of algae was evident. The coincidence of high algal density with high recruitment peaks in the winter and low algal density with low recruitment in the summer made the seasonality even more pronounced.

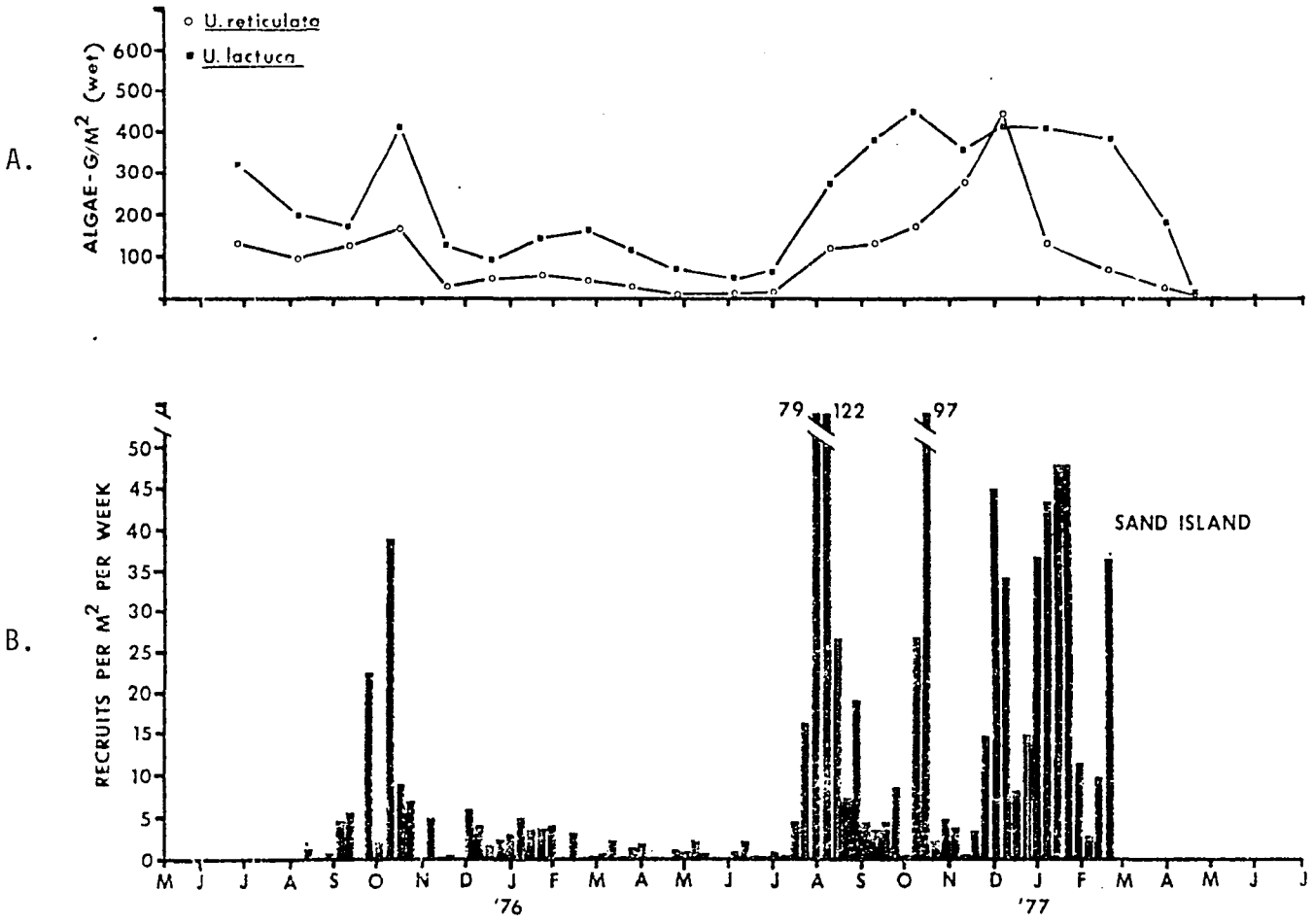

Figure 22 A. Standing crop of U. reticulata and U. lactuca at Sand Island in wet weight.

B. Total weekly recruitment rate per square meter at Sand Island.

Discussion.

Typically, recruitment is compared with adult density (or fecundity) by reporting both as functions of bottom area. However, because juveniles of Aplysia juliana live in a different habitat from the adults (i.e. on algal rather than rock and gravel substrata), there is a rationale for considering their populations separately from those of adults. Examining recruitment as a function of algal density allows insights into several important questions. The first is whether variations in observed recruitment rates reflect variations in larval abundance in the plankton (i.e. variation in number of "recruitable larvae") or variations in algal density (i.e. variation in amount of recruitment space). The seasonal variation in recruitment rates expressed as a function of 100 g of algae shows there is considerable variation in larval abundance (Figure 21). In addition, the enhancement of this seasonality when recruitment was expressed as a function of area shows that variation in algal density affects the numbers recruited to the study area (Figure 22).

Settling substances produced by preferred substrata have been shown to affect the larval settling in many invertebrate species (Crisp 1974). Larger quantities of algae could cause increases in settling due to greater concentrations of settling substances being released into the water. If recruitment rates were influenced by increased concentrations of settling substances caused by denser crops of Ulva, one would expect higher rates of recruitment at locations with larger crops of algae, but this is not the case. Recruitment rates were always higher at Kewalo which had a very small crop of Ulva compared to Sand Island.

Recruitment of A. juliana occurred throughout the year, although at higher rates in the fall and winter than in spring and summer (see Figure 22). Weekly recruitment whether expressed as number per square meter or number per 100 g of algae revealed the same relationship. Such seasonality in recruitment can be a function of the life history of the species as well as a response to the physical aspects of the environment. The opisthobranchs have varied life history patterns. Miller (1962) divided nudibranchs into two groups and Clark (1975) devised a similar system, labeling the first group strategists and the second exploitists. The strategists have late, seasonal reproduction with recruitment confined to a brief period and have a K-reproductive strategy. The exploitists have early, continuous reproduction, with continuous recruitment and a r_o-reproductive strategy. A. juliana falls under the exploitist category, with individuals reproducing continuously from an early age and with a life span of less than one year.

Usuki (1970) reported that A. juliana in the sea of Japan had seasonal reproduction and recruited only in May and June. The differences between the biology of A. juliana in Hawaii and in the seasonally colder waters of Japan show how environment can dictate the reproductive patterns of these animals.

For A. juliana the sizes and fecundities of adult populations and recruitment rates are ultimately related to the seasonal fluctuations of the Ulva crop although the interrelationships are very complicated. At some times the effect of the crop of Ulva on

recruitment is probably negligible compared to the effect of fluctuations in larval density in the nearshore waters. When there is little or no algae, the algae crop may completely define the intensity of recruitment in a particular habitat. Algal density also affects the reproductive output of a population by controlling the growth of individuals in that population; larger animals lay proportionately more eggs.

Recruitment in A. juliana is characterized by the occurrence of very large influxes of larvae (see Figure 21). Large pulses last but a few days and, excluding summer when recruitment is always low, seem to occur randomly throughout the year. In addition, comparing recruitment rates on U. reticulata at Kewalo and Sand Island (Figure 21), one can see that some large settlement pulses occurred concurrently at Kewalo and Sand Island while others did not. The natural history of the larvae and characteristics of inshore water flow which carries the larvae may help to explain the large day to day variability in recruitment.

Larvae of A. juliana have been grown to metamorphic competence in about 30 days but they can also delay metamorphosis for up to 80 days (Switzer-Dunlap and Hadfield 1977). During this period the larvae drift passively wherever the water currents take them. A great many of these larvae must be carried out to sea and die.

The movement of inshore and offshore water masses determine the location of competent larvae. Even though the prevailing winds in Hawaii blow to the west, the currents form a confused and variable

pattern between the islands. Patzert (1969) discussed the existence of large (50-150 km in diameter) cyclonic and anti-cyclonic eddies found during all seasons in the lee of the Hawaiian Islands. These eddies can last from two weeks to two months and cause the entrainment of locally produced larvae. Aplysia larvae could spend a month in the circulation patterns among the islands and still be in the vicinity of land when they were ready to metamorphose. The unpredictable nearshore currents and tidal currents could then bring the larvae nearer to shore. The variability of these offshore currents combined with variability of nearshore currents might therefore explain the day to day variability in recruitment as well as why pulses do not always occur simultaneously at separate but close locations.

Physical factors such as tides, wave action and storms could affect day to day settlement rates by causing increased water flow over the reef areas and thus bringing more larvae into contact with algae. Storms and unusually high surf were recorded on a tide calendar and compared to recruitment patterns. No correlation was found between wave action, storm activity, or phase of the moon and observed settlement peaks. These factors could no doubt modify the success of settlement pulses but do not appear to initiate or cause them.

There are several mechanisms which could bring about differences in recruitment rates between locations, although few could be easily tested. The Ulva from one location might be a more potent cue for settling, but competent laboratory reared larvae settled on all types

of Ulva in equal proportions. Another possible mechanism could be higher concentration of larvae in the water near Kewalo than occurs at Sand Island. The two sites were only about 5 km apart and there were no major coastal features between the two. Although the inshore circulation could be quite different at the two locations, it is doubtful that there were any major differences in the origin of the water that flowed over the two areas. Wyrtki, et al. (1969) studied current patterns around the Hawaiian Islands and stated that the currents around the islands were very erratic and highly unpredictable.

A third possible mechanism for explaining differences in recruitment rates between locations is that the water at both locations had, on the average, the same numbers of larvae but that the physical aspects of the Kewalo area allowed for a more successful settlement rate. Hatton (1938) observed that settlement of Balanus balanoides at St. Malo was higher in areas of moderate current or waves than those in calm areas. He postulated that more water flowing across an area would bring more larvae to the area and would increase settlement. This idea was supported by the fact that recruitment was higher on bare surfaces than under large algae. Supposedly the algae served to reduce circulation and thereby reduce settling although the algae rubbing on the rocks might tend to scrape off settling cyprids.

For A. juliana there would be a trade-off between increased current bringing more larvae into contact with the algae and increased current or wave shock that would keep the larvae from settling and holding onto the substrate. When these larvae attach to Ulva and begin the process of metamorphosis, the attachment point is very small

and weak. Water squirted from a pasteur pipette can easily dislodge the juveniles in this stage. Wave shock which could easily dislodge juvenile A. juliana is much higher at Sand Island along with higher water flow over the algae. It is not possible to discern which factors are most influential on recruitment without more experimentation; it does seem, however, that the calmer of the two locations has higher rates of recruitment.

In order to calculate planktonic survivorship in A. juliana, we must first assume no significant recruitment from outside the Hawaiian Islands and that survivorship calculated at Sand Island and Kewalo is representative for the species in Hawaii. Secondly, it must be assumed that the fecundity calculated for animals at Sand Island is a reasonable estimate for the species in general. Since fecundity appears to be a function of body size rather than of aspects of the habitat, fecundity rates can be established using figures from the caged animals. If an animal lives for one month, it can be expected to lay 22% of its weight in eggs, 85% in two months, 137% in three months, and 202% if it lives for four months.

Estimates for lifetime fecundity of A. juliana in Hawaii vary from 2.49×10^6 to 48×10^6, the lower figure being an estimate for an animal achieving a maximum weight of 10 g and living for two months and the upper figure being the fecundity observed in the caged animals. Since only one successful recruit which lives to reproduce is necessary to affect replacement, only about 4.02×10^{-7} to 2.08×10^{-8}% of the larvae will survive to reproduce and since less than 2% of the recruited

juveniles survive to reproduce, about 8.04×10^{-5} to 4.16×10^{-6}% will live through the larval period. Estimates of yearly larval survival for other species include 3% for the snail Lacuna sp. (Smith, 1973), .02% for the barnacle Balanus balanoides (Pyefinch, 1948), .05% for the shrimp Penaeus duorarum (Monroe, 1968) and .0017% for the gorgonian Eunacella stricta (Theodor, 1963). The estimated survival rates for A. juliana were much lower than any of these.

One might expect high initial rates of mortality which would decrease as the animals grew. Survivorship of juvenile A. juliana shows this relationship to some extent, in that mortality is initially higher on U. reticulata from Kewalo and U. lactuca from Sand Island. Survival on U. reticulata from Sand Island shows constant mortality throughout this period (see Figure 20). The high rates of mortality shown after 20 days could be due to juveniles leaving the algae for the adult habitat or both. Although the data show a slightly higher initial mortality rate, the overall appearance is more of a Type 2 survivorship curve (Pearl 1928) characterized by constant mortality than a Type 1 curve which indicates very high initial mortality rates. If larval mortality were also considered, then the Type 1 curve would best represent A. juliana.

The causes of juvenile mortality are probably many, including both biotic and abiotic factors. MacGinitie (1934) reported flatworms, nemertines, annelids, crabs, isopods, hermit crabs and some fish to eat A. californica. Several animal species were implicated as possible predators on A. juliana. The wrasse Thalasoma duperei and another

and another unidentified wrasse were seen picking juvenile slugs off Ulva in the field and would also readily eat them in the laboratory. Thalasoma duperei is one of the most common fish in the nearshore habitat and could possibly significantly reduce the numbers of Aplysia on the algae. The hermit crab Dardanus sp. and the gastropod Conus pennaceus have also been seen eating small slugs in the field. Other animals that readily ate Aplysia in the laboratory were the crab Calappa sp. and two flatworm species. There are undoubtedly many other animals that prey on these small slugs.

The abiotic factors which affect the algae they live on could also add to the mortality of small aplysiids. Sections of Ulva become reproductive and slough off the parent plant along with any animals that might be on them. Large amounts of Ulva are torn loose during storms; it is not uncommon to find Ulva piled up 1/2 m deep after a storm. Probably the most significant source of mortality is that due to animals being dislodged from the algae by wave action or getting scraped off by algae rubbing together in wave surge. The wave shock in all the areas studied was quite high.

Juvenile A. juliana have a behavioral pattern that might tend to reduce mortality due to the above factors. After they have started feeding and crawling, the juveniles begin to migrate towards the denser parts of the algae. Because of this movement juveniles congregate near the bases of the plants. If they are on U. fasciata or U. lactuca or in the thicker more tangled parts of U. reticulata. Losses from predation and wave shock are probably lower in these areas. As was stated earlier, in the laboratory where these sources of mortality do not exist, survivorship is essentially 100%.

The planktonic period is undoubtedly the time of highest mortality for A. juliana. The larvae are not only exposed to heavy predation during their one month or longer stay in the plankton, but also have a high probability of being swept away from the islands. Even the individuals that remain near the islands stand a poor chance of encountering Ulva. Less than 2% of the animals that settle live to reproduce. Aplysia juliana offsets these losses by producing large numbers of eggs.

CHAPTER IV

Demography

Introduction.

Rapid, dramatic changes in population size have been reported for many opisthobranchs (Alder and Hancock 1845; Balch 1908; Chambers 1934; Costello 1938; Swennen 1961; Miller 1962; Thompson 1964; Nybakken 1974; Clark 1975). Although the mechanisms and reasons for these fluctuations are unclear, they are often attributed to fluctuations in abundance of food (Miller 1962; Clark 1975; Swennen 1961) or to changing temperature which may affect stability by limiting reproductive success and/or growth (Clark 1975).

However, most studies have been made in temperate latitudes and habitats in more tropical areas are thought to be less harsh and to support more stable populations than those in more temperate areas. At the beginning of this study, it was thought that the Hawaiian populations of A. juliana would follow this generalization with relatively constant rates of recruitment and mortality. It soon became obvious that very little associated with this animal was constant.

Recruitment rates and survivorship of animals in larval, juvenile, and adult stages will all affect population size and stability. Factors which can affect recruitment and survivorship are algal density, population fecundity, weather, and predation pressure. This study will examine these factors for their effects on the density and size distribution.

Methods.

The main study site was an area of about 900 m^2, centered approximately 10 m from high tide line at Sand Island, Oahu, Hawaii. The depth ranged from 0 to 1 m at low tide. The bottom was primarily large rubble with areas of sand and gravel and some flat rock.

Two secondary sites were also studied. One was an area of about 20 m^2 at Black Point, Oahu. The area was isolated by sand on one side and a vast expanse of flat table rock on the other. The bottom was sandy with areas of flat rock. There were many rocks under which the aplysia lived. The dominant alga was U. fasciata. The other site was located along the shoreline in the Ala Moana area. Here the animals were found in very shallow water within 1-2 m of the shore. The area was characterized by a gravel bottom with many large and medium sized rocks. The algae found here were U. lactuca and some U. reticulata a little farther off shore.

Monthly, weather and tides permitting, a 10 m transect was arbitrarily laid down in the Sand Island area and for .75 m on either side, animals and eggs were collected from the gravel and from under rocks. The area being sampled was greatly disturbed by turning over all the rocks and fanning up the gravel. A week or two for transected areas to recover and for this reason the technique of random sampling was used instead of employing a fixed transect.

The animals and eggs were taken to the laboratory and weighed and the animals were returned to the field. Care was always taken to put the animals back under rocks so they would not be swept away. Animal

density, size distribution and fecundity were monitored. Algal standing crop of U. reticulata and U. lactuca were also monitored (see methods section of Chapter III).

The populations at Black Point and Ala Moana were monitored for size distribution of A. juliana and subjective estimates of relative algal and animal density were made.

Results from other experiments described earlier were also used here to evaluate the field populations and various factors which affected their growth, longevity and numbers. Results from experiments with caged animals and released spotted animals are discussed here to clarify observed trends in densities and stability of field populations.

Results.

Animal Density. Densities of adult A. juliana were extremely variable through time at all sites examined. Figure 23 illustrates the change in population density at Sand Island during the time of the study. There was a marked seasonality with densities below 1.0/m^2 in the late summer and fall and much higher values, up to 3.5/m^2, in winter and spring. The populations went extinct twice (9/75 and 5/77) and dropped very low in 8/76.

Although the densities of A. juliana at Black Point and Ala Moana were not measured they appeared to be comparable to those at Sand Island at certain times. The habitats at Ala Moana and Black Point were much smaller and the populations in those locations were also very small compared to those at Sand Island.

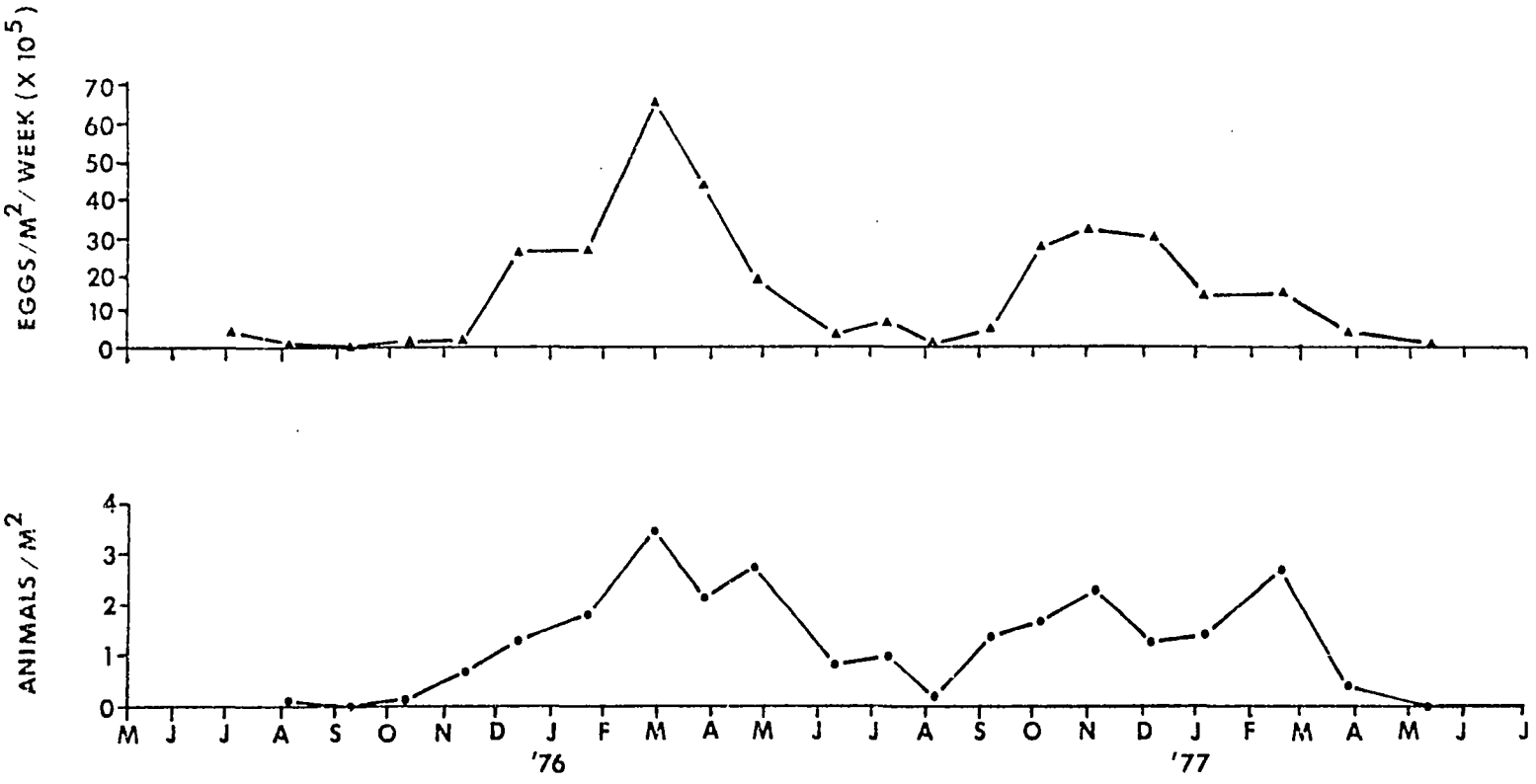

Figure 23. Density and fecundity of a population of A. juliana at Sand Island over an 18 month period.

The populations at Black Point and Ala Moana were intermittent and unpredictable except that during May, June and July there were no animals at either location. Figure 24 shows the distributions of sizes of A. juliana during months when animals were found at Black Point. The population thrived for the first nine months of sampling and then disappeared for seven months. A population reappeared in November for about a month and then disappeared again. No animals have been seen there since.

Populations at Ala Moana were even more unstable and short lived than those at Black Point. As Figure 25 shows, one population lasted only long enough to be sampled once in November 1974. Another population was detected on 2/28/76 although no size-distribution data were taken until 3/5/76. This population was last sampled on 4/4/76 and by 5/3/76 it was gone. The third population was detected on 1/26/76 and again on 2/21/76; by 3/30/76 it was gone except for two animals. These populations seemed to have life spans of two to three months or less. Similar short lived populations were seen at other locations around Oahu.

Size Distributions. Size distribution also proved to be quite variable at Sand Island. Animals reached larger sizes in late winter and early spring (see Figures 26, 27, and 28). These times correspond to times when the algal densities were highest and water temperatures were coldest.

The animals at Ala Moana and Black Point were always smaller on the average than those at Sand Island and seldom attained sizes over 20 g.

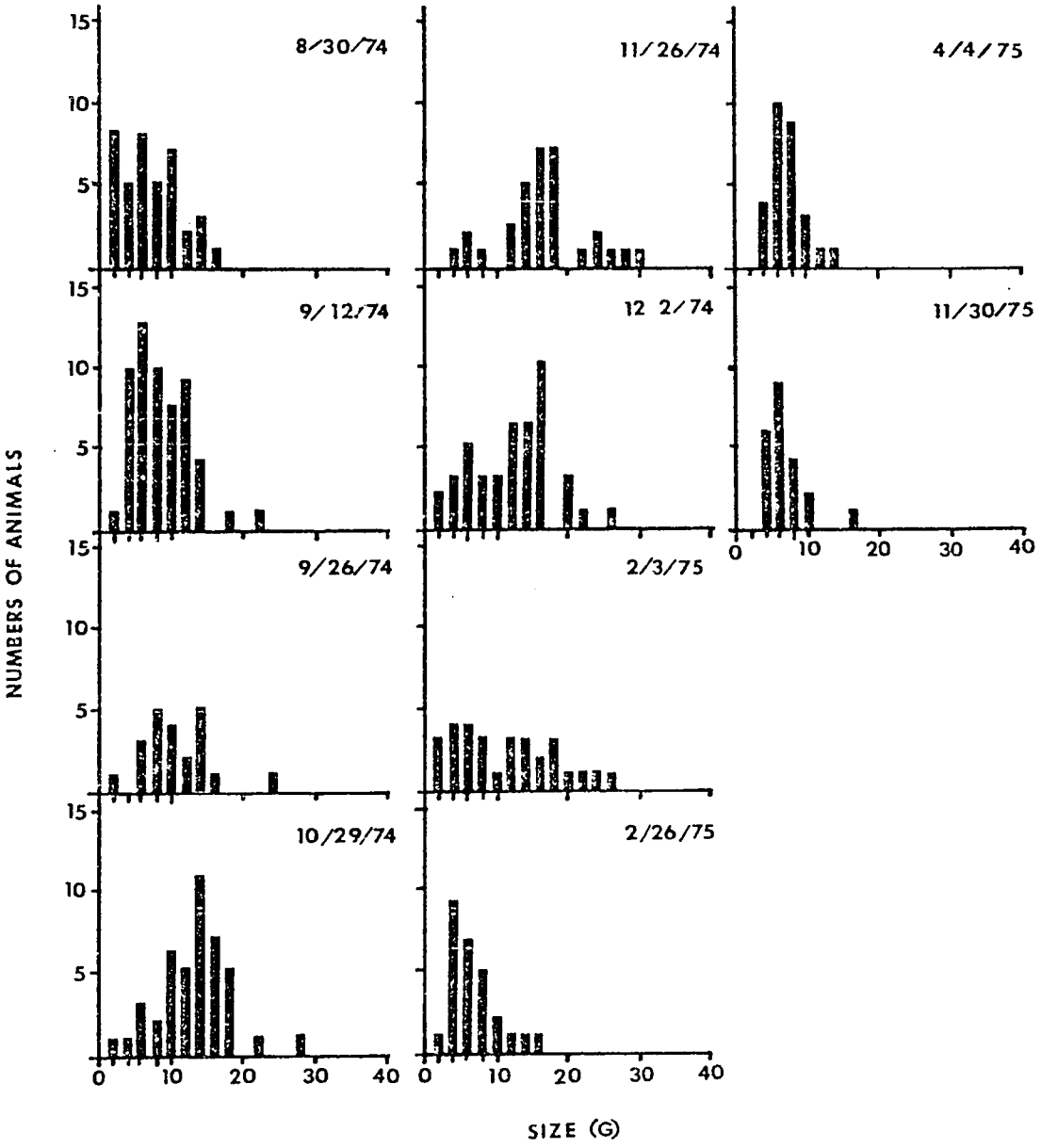

Figure 24. Monthly size distributions for A. juliana at Black Point.

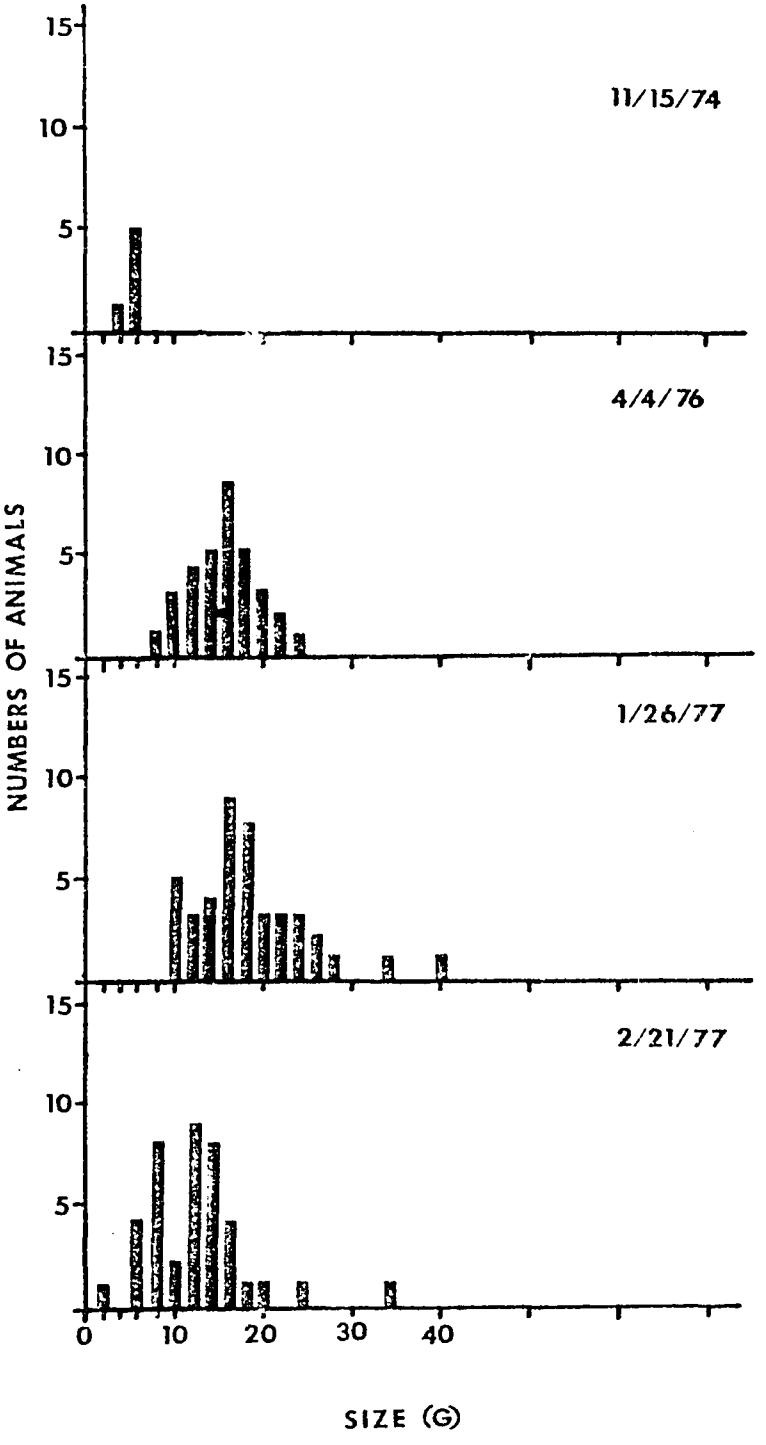

Figure 25. Monthly size distributions for A. juliana at Ala Moana.

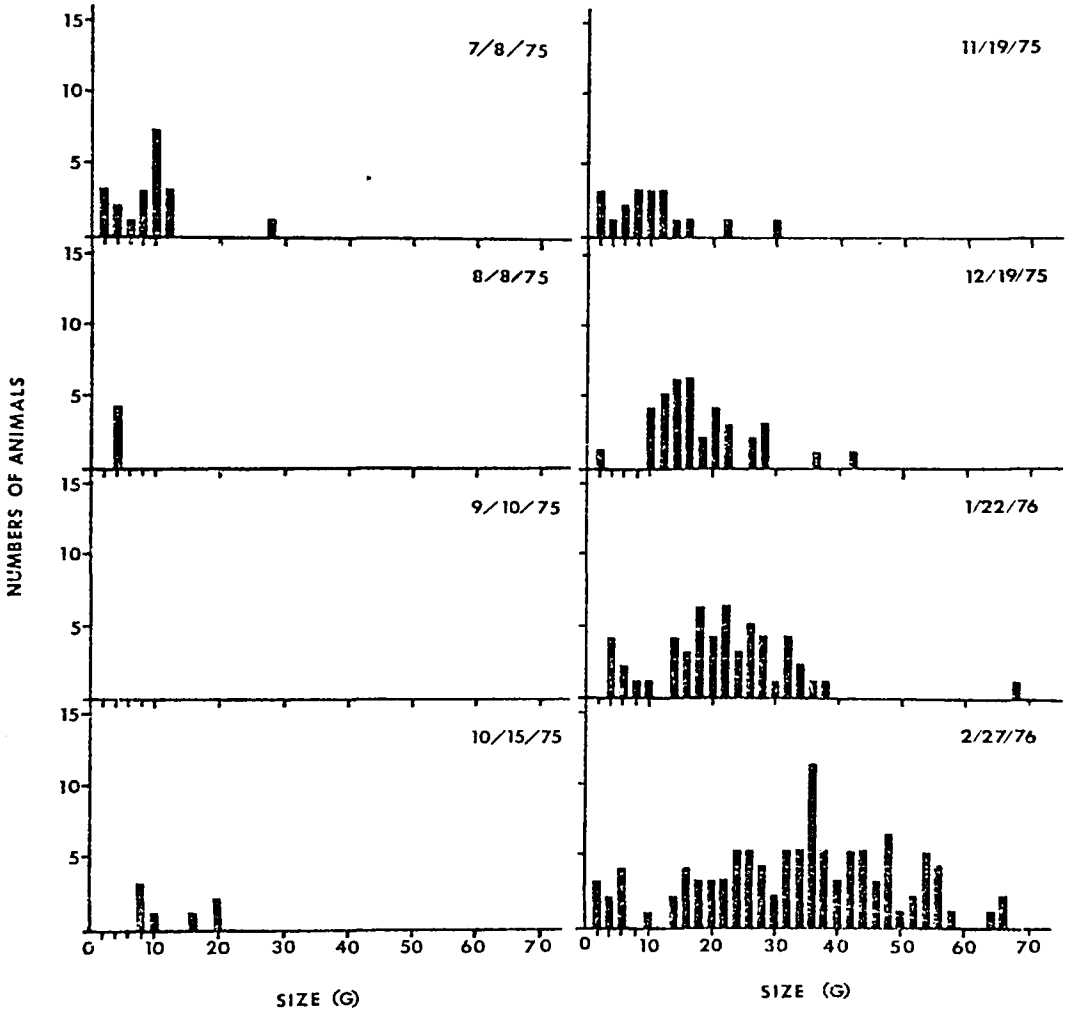

Figure 26. Monthly size distributions for A. juliana at Sand Island. (7/8/75 through 2/27/76)

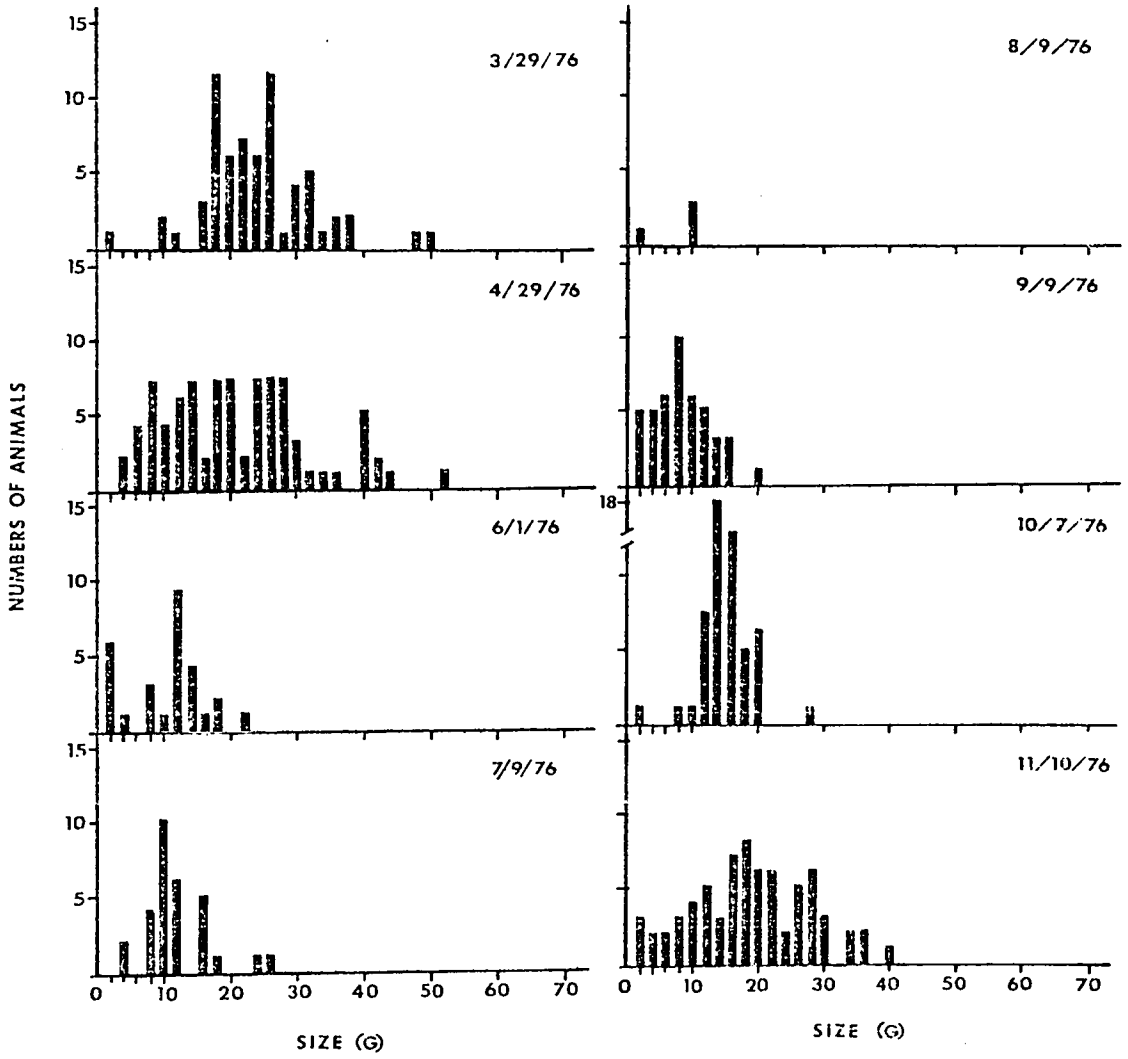

Figure 27. Monthly size distributions for A. juliana at Sand Island. (3/29/76 through 11/10/76)

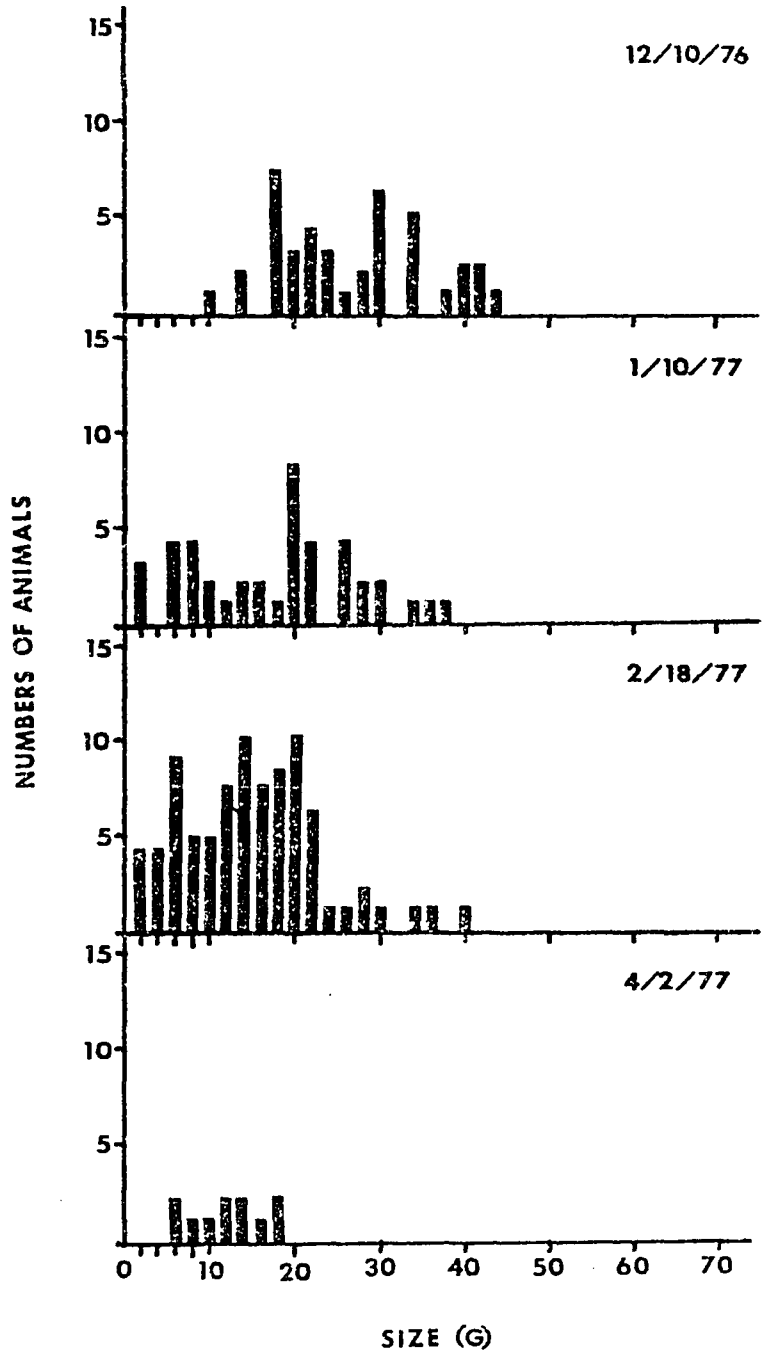

Figure 28. Monthly size distributions for A. juliana at Sand Island. (12/10/76 through 4/2/77)

These animals, though much smaller, were reproductive adults. It was not uncommon to find animals 3 to 5 grams in weight that were reproductive, which was in contrast to the animals at Sand Island which were never reproductive at such small sizes.

Algal Standing Crop. The variations in the density of the Ulva crop at Sand Island were discussed in Chapter III (see Figure 22). Subjectively, Ulva was always plentiful except for one period in May of 1977. This was the only time when the algal density was too low to support a population of Aplysia. This was a rare occurrence and at any other time it would be hard to imagine an established population being limited by algal abundance.

The algal density at Ala Moana was always relatively low and while there was variation, it did not seem to follow variations at other locations. Standing crop was measured twice at times when it was especially dense and averaged 10.1 and 15.2 g/m^2 (wet). These figures are very low compared to those at Sand Island.

A dense healthy crop of Ulva at Black Point persisted until the summer of 1975 and then declined in volume until it completely disappeared by fall. Algae were seen again for a couple of months in midsummer of 1976 but had disappeared again by fall and have not been since reestablished. Radical variations in algal crops have been seen at several other locations around Oahu. There can be no populations of A. juliana without Ulva.

Fecundity of Animals in the Field. Fecundity was calculated for the field population at Sand Island for each of the monthly samples (Table 1). Fecundity was expressed as a percentage of the total animal weight per day to make it comparable to laboratory and cage experiments and as a function of area per week to be comparable to recruitment rates. There is a great deal of seasonal variation in the fecundity of the population although the fecundity relative to population biomass was fairly constant (2.23 ± .88% (std. dev.) of the total biomass). Individual animals have the same fecundity rate regardless of season.

Fecundity of a set of caged field animals is shown in Table 2. Fecundity was highest in the early part of their lives and declined as they aged; averaging 2.33% of their body weight per day. This is the same as the rate that was measured for the populations sampled by the transects even though the caged animals were larger.

Fecundity was not monitored for the Black Point or Ala Moana population but judging from the size and numbers of egg masses seen, the fecundity rate would not appear to be different from that measured at Sand Island.

Adult Survival in the Field. Assessment of adult survivorship in the field was hindered by two complicating problems. The first was that no satisfactory method for following individuals in the field was devised (see Methods, Chapter II). The second was constant recruitment to the population. Following cohorts was difficult because they were masked by constant new additions to the population. There were two cases in the Sand Island size distribution data where it

TABLE 1

Monthly Fecundity Estimates for a Population of *A. juliana* at Sand Island

Sample Date	Total Weight of Animals (g)	Total Eggs (g)	Fecundity % Total Animal Wt/Day	Fecundity $G/M^2/Wk.$	Fecundity $Eggs/M^2/Wk\ (x\ 10^6)$
7/8/75	197.8	38.41	2.77	.85	.34
8/8	21.41	2.66	1.78	.077	.031
9/10	0	0	0	0	0
10/15	95.7	15.41	2.3	.34	.14
11/19	172.87	12.39	1.02	.41	.16
12/19	935.4	193	2.96	6.43	2.57
1/22/76	1339.5	275.1	2.93	9.17	3.67
2/29	3413	492	2.1	16.4	6.56
3/29	1349	326	3.45	10.58	4.35
4/29	1839	139.2	1.08	4.64	1.86
5/25	268	25.97	1.38	.87	.35
7/9	329.7	47	2.05	1.57	.63
8/9	20.48	4.0	2.79	.13	.052
9/10	329	31.94	1.39	1.06	.42
10/8	708	200.1	4.04	6.66	2.66
11/10	1256	238	2.7	7.93	3.17
12/10	980	222	3.25	7.4	2.96
1/10/77	707	104.0	2.12	3.5	1.4
2/18	1200	109.6	1.3	3.63	1.45
4/2	120.7	27.3	3.23	.9	.36
5/7	0	0	0	0	0

Mean 2.23 ± .88 (std. dev.)

Table 2

Fecundity Data for Animals Grown in a Cage at Sand Island
(N = 5)

Sampling Date	Average Weight (g) of Animals	Eggs Laid Per Animal per Week (g)	Eggs Laid as % of Body Weight Per Day
11/26/76	1.11	--	--
12/2	10/68	--	--
12/9	23.6	--	--
12/16	34.4	1.48	.73
12/23	41.44	4.6	1.73
12/30	47.7	10.52	3.37
1/6/77	49.0	10.34	3.06
1/13	51.0	11.04	3.15
1/20	50.0	11.56	3.32
1/28	51.28	9.0	2.51
2/3	54.2	7.52	1.99
2/10	50.4	7.82	2.21
2/17	56.5	7.82	1.90
2/24	62.2	9.9	2.27
3/3	59.75	9.42	2.25
3/10	66.6	10.1	2.18
3/17	70.0	9.53	1.94
3/28	59.0	8.75	2.12
		Total 607.56	Mean 2.33 $\pm$ .72

appeared that a leading edge of a new population could be followed (see Figures 26 and 27). One was from 11/19/75 through 2/27/76 and theother was from 9/9/76 through 12/10/76. In both cases an estimate for the life span of the cohort would be about three months. However, there were many instances, especially at Black Point and Ala Moana, where a population lasted for only one or two months. It appears that population survivorship is quite variable from time to time and from place to place.

The cohort of spotted A. juliana released in the field at Sand Island showed high mortality in the first week and then maintained fairly constant numbers for 2-1/2 months. Thus, it seems that once an individual A. juliana gets established in the adult habitat it is relatively safe. Death due to predation is probably very rare; the only cases of adult mortality have been reports of fishermen spearing them. Storms and wave action are probably the cause of most larval and adult mortality.

Discussion.

The life history of A. jul ıa can be divided into three fairly distinct periods: the larval period, about which we know very little; the three week juvenile period, spent on the algae, which was discussed in Chapters II and III; and the adult period most of which is spent under rocks. The selective pressures and factors affecting survival are different for each of these periods and will result in different strategies for each. In this chapter we are dealing only with variations in adult populations.

Some species such as A. juliana have evolved characteristics which allow them to survive in widely fluctuating environments. Analysis of life history features such as time to first reproduction, fecundity, and survivorship should reflect the ways in which species adapt to such environments.

The volume of recruitment to any population of A. juliana is a function of the number of competent larvae in the plankton and the amount of substrate available for settlement (Chapter III). For A. juliana the amount of available substrate for settlement changes as the density of Ulva changes (Figure 22). Since there were competent larvae in the plankton during the period when Ulva was absent from the Kewalo habitat (see Figure 21), the availability of substrate can greatly affect the recruitment to and subsequent size of the population there. This is of course an extreme case, but the relationship of recruitment and algal density no doubt exists under more normal situations.

The intensity of the juvenile mortality while on the algae significantly modifies recruitment to the population. The survivorship rates discussed in Chapter III are average figures derived by summing data over a long period of time. By comparing the recruitment rates (Figure 22), adult densities (Figure 23), and size distribution data (Figure 24, 25), it becomes clear that juvenile survivorship much vary considerably. Large peaks of recruitment are not necessarily followed by abrupt rises in adult numbers or larger proportions of smaller animals in the samples. Furthermore, the highest adult densities (February 1976) occurred during periods of relatively low recruitment and one of the lowest levels of adult densities (September 1976) was during the highest peak of recruitment seen.

Spight (1974) quotes Paine (1966), Paine and Vadas (1969) and Dayton (1971) to support his contention that the suitability of marine intertidal habitats change continuously as predation intensity and climatic stresses vary; changes in the composition of the site's fauna follow. Often, in successional situations, the animals themselves make the habitat unfavorable to future populations. Fugitive or colonizing species take advantage of these fluctuations to provide new habitat and Spight (1974) goes so far as to say "all species depend upon the asynchrony of changes in adjacent habitats" and that a species "must continuously disperse in search of newly suitable habitats". With so much randomness and asynchrony in habitats, local extinctions should not be a rare event. Spight (1974) and Erlich (1965) discuss such extinctions and cite examples.

A. juliana exhibits many of the appropriate characters for a colonizing species. Its life history is inexorably linked to the presence of Ulva which is itself a classical colonizing species. Matching the variability of a food species with variability of recruitment and survivorship of a prey species results in a highly unstable situation. This instability results in highly unstable situations. This instability results in highly unstable populations which experience frequent extinctions. In addition, many of the habitats of A. juliana, such as those at Ala Moana and Black Point, are very small and support only small numbers of animals which make them more susceptible to extinction. Populations at these two spots showed greater instability and thus more frequently extinct than the larger populations at Sand Island.

Species such as A. juliana which have a high probability of local extinctions depend on other areas within their range of dispersal becoming favorable. As discussed earlier, A. juliana is an extremely fecund animal which starts reproducing very early in life. These factors along with a relatively long planktonic period allow the species to disperse widely and take advantage of new favorable habitats.

The size distribution data support the notion that adult survival is relatively high. Aplysia juliana populations are adult dominated with very few small, prereproductive animals. Adult dominated populations have been reported for the starfish Linckia laevigata (Yamaguchi, 1977; Laxon, 1974), Acanthaster planci (Branham, et al., 1971; Wilson and Marsh, 1974), and the clam Tridacna spp. (Asano, 1937; Motoda, 1938;

Hester and Jones, 1974; McMichael 1974). Yamaguchi (1977) states that the apparent paucity of juveniles within the adult population characterizes many larger benthic animals in coral reef habitats and that this is a result of high survivorship and long life in the adults and very low rates of recruitment or only occasional recruitment success. This sort of distribution is exaggerated by the rapid growth of smaller animals. The time spent in these smaller size classes is short and there is little chance of finding small animals.

Juvenile A. juliana, like starfish and many other reef animals, live in habitats different from those of adults. Along with their small size this makes them difficult to census. If one searched only the adult habitat, small aplysias would never be found. There were many very small A. juliana in the habitat but it took a special technique to detect their numbers.

Division of animals into size classes rather than age classes can result in an appearance of adult dominated populations. If an age distribution were heavily weighted toward the older animals, the population would be moving toward extinction. But, with Aplysia and probably other animals, it is difficult if not impossible to obtain a reliable means of assessing age of field animals. The size of an Aplysia, being affected by temperature and access to food, cannot be translated directly to age.

A small number of juveniles in the samples can also be a result of large but relatively rare recruitment success (Yamaguchi 1977). Variability in both rate of recruitment and success of those recruits

establishing themselves may also contribute to the appearance of an adult-dominated population as shown by A. juliana. Since the sampling spanned many generations of this animal, it is unlikely that this type of size distribution is a result of rare recruitment success. Rather, it is probably a result of rapid growth in the juveniles.

One might expect food abundance to affect population size as well as growth and fecundity of the animals within it. Food density will obviously affect the number of animals recruiting into the population if their larvae are induced to settle by the food substance. But once a population is established, variation in food abundance--short of its total absence--may not affect the size of the population. Paine (1965) reported that food did not seem to limit abundance of Navanax once the population was established and Spight (1974) stated that all populations of Thais spp. were food limited in growth and fecundity but not in survival. Choat (1977) also found that density, and thus availability, of food affected growth but not survival in limpets. It seems that the density of Ulva can affect the size of the populations through limiting recruitment but probably does not in most cases affect the survivorship of the populations once they are established.

Determining survivorship in the field proved to be very difficult for many of the same reasons which complicated efforts to measure field growth. All forms of individual tagging were unsuccessful, constant recruitment obscurred the growth of cohorts and variations in size distributions within and between populations made analysis of

density and size distribution data difficult. The only direct data on survivorship of a known group of field animals was from the spotted animals released at Sand Island (see Figure 4, Chapter II). In this group there was a high initial mortality, followed by a long period of high survival and a rapid die-off after about two months. The mean life span of this group was 25 days. It must be remembered that adult survivorship of A. juliana varies greatly from time to time and place to place and the above is just one estimate for a particular time and place. Whole populations have become established and disappeared within the space of one to two months.

Judging by the wide variation in life spans of different populations of A. juliana, it is probable that the life expectancy for individuals in those populations varies also. Populations last from one or two months to a year. Life expectancy for individuals in these populations could vary from a few weeks in populations of the shorter duration to a maximum of three months as shown by the caged animals.

Juveniles and small adults are probably subject to both biotic and physical forms of mortality while the larger animals are more affected by physical factors. There are several predators which could prey on small aplysias weighing up to 2 g, but once they have grown larger, there are few, if any, predators. Storms and high waves are the most powerful factors threatening these animals. The differences in survival between the two tanks in the current experiment (Chapter II) showed how water movement can increase mortality. Once an animal loses

its hold it could easily be swept out of the habitat or battered to death. Large storms often dislodge rocks and stir up gravel depriving the slugs of their hiding places. On occasion, storms have completely covered large areas with a thick layer of gravel surely killing the animals buried beneath it and eliminating habitat for others. Ulva cannot get established on gravel. Even the ordinary amount of wave action could take its toll on these aplysias, especially when they become more active and come out at night to forage.

Experiments conducted in the laboratory have shown that under ideal conditions A. juliana can live for six to seven months. This figure is probably the maximum potential limit for this species at local temperatures. Aplysia juliana in the field probably never realize their potential life span. The wave swept, shallow, habitat is a very rigorous environment and probably serves to shorten their life expectancy. The maximum life span observed in the field was 3-1/2 months and was for animals grown in the cage (see Figure 26).

CHAPTER V

ENERGETICS

Introduction.

Energy obtained through feeding may be used for growth, reproduction and metabolism, or it may be lost as waste. What determines the allocation of energy to these various fates is poorly understood. The ways in which animals acquire and handle energy are quite variable and depend heavily on the selective pressures acting on any particular species. There is also much to be learned from studying how the allocation of energy changes as a particular animal ages. One can ask: How much and when does it reproduce? What percentage of its energy budget is used for maintenance? Does the relationship of energy to growth and reproduction change with age or feeding ration? In the following studies the energetics of A. juliana will be examined with regard to the above questions.

Methods.

In order to establish an energy budget one must estimate: 1) energy of food ingested, measured by weight of food eaten; 2) energy to growth, measured by weight gain; 3) energy to reproduction, measured by weight of spawn; 4) energy to metabolism, measured by respiratory rate, and; 5) energy lost to feces measured in weight of excretion. All measured parameters are generally converted to calories.

Wet-Dry Wet Conversion. Wet/dry weight conversions for body tissue, eggs, and algae were obtained by first rinsing the sample in fresh water to remove salt, damp drying, weighing and then drying in a dessicating oven at 60° C until a constant weight was obtained. A reliable figure for wet weight of feces could not be obtained.

Ash-Free Conversion. Ash free dry weights were obtained for monthly samples of U. lactuca-raised animals ranging in weight from .025 to 50.0 g, spawn, and feces by ashing weighed dry samples in a 500° C muffle furnace for three hours.

Calorimetry. The methodology for determining the caloric content of biological substances was based on procedures established for micro-bomb calorimetry by Paine (1964, 1966) and Phillipson (1964). The apparatus employed in this study was a Phillipson oxygen micro-bomb calorimeter capable of measuring samples weighing from 2 to 20 mg. Samples used varied in weight from 10 to 20 mg.

Respiration. Respiration rates were obtained by monitoring O_2 consumption with a Yellow Springs Instrument Model 54 oxygen meter. Animals of sizes ranging from .048 to 50.0 g were tested. The size of container and number of animals used per experiment were varied so that each experiment lasted from 30 to 45 minutes. The chambers consisted of 50, 250, and 600 ml beakers with stirring bars to insure adequate mixing. A round piece of plastic mesh fitted into the beaker kept the animal away from the stirring bar. The tops of the beakers were heated

and pressed into pieces of 2 cm thick styrofoam to make form fitting tops for the vessels. A hole was cut in the top for insertion of the oxygen probe.

All animals used were well fed and all runs were done at 25^{o} C. The specimens were placed in beakers of aerated seawater and given several minutes to acclimate. Once an animal ceased crawling about, the beaker top was put in place and the experiment begun. Oxygen levels were read at two minutes and subsequently at five minute intervals until oxygen level had dropped below 3.0 ppm.

Three controls were conducted using seawater without animals to determine bacterial respiration but after 45 minutes there was no detectable drop in oxygen concentration.

Caloric equivalents for respiration were obtained by converting to calories/animal/hour by the following formula:

$$\text{metabolism} = (O_2 \text{ start (ppm)} - O_2 \text{ finish (ppm)}) \times (\text{volume of container (l)}) \times (1 \text{ mg } O_2/1 \text{ ppm/liter}) \times (.7 \text{ ml } O_2/\text{mg } O_2) \times (4.89 \text{ cal/ml } O_2)$$

(Winberg 1956).

Fecal output was not monitored in any of the long term feeding studies; therefore, a separate experiment was performed to estimate the amount of feces produced from a known amount of food. Since most of the feeding studies used U. lactuca as food, this alga was employed here also. Eight animals, with weights from 19.6 to 40.9 g, were starved overnight, one animal was dissected to ensure that guts were empty at the start of the experiment, and the remainder were divided

into two groups of two and one group of three. These animals were placed in large aerated fingerbowls with known amounts of algae and left to feed for three hours.

The first feces were passed after 75 minutes and feces were collected at 20 to 30 minute intervals until 5 hours after the food was removed. At this time two animals were dissected and both had empty guts. The feces were collected on Millepore Prefilters which had been dried at 60^{o} C and preweighed. The feces and filter were rinsed to remove any excess salt and dried at 60^{o} C to a constant weight. The weight of the filter was then subtracted and samples of the fecal material were used to determine ash and caloric contents.

Two techniques were used to estimate caloric content, the first being bomb calorimetry. Fecal samples would not combust, presumably because of high salt content, which necessitated mixing samples with known amounts of benzoic acid. The caloric values obtained were very low and thus a second method was utilized to double check these findings. This technique was the wet oxidation method outlined by Russel-Hunter, et al. (1968). Similar very low caloric values for fecal material were obtained by the second method as well.

Many of the growth studies discussed in Chapter II were analyzed using the caloric values obtained here. A short experiment was also done to analyze the effect of starvation on egg production. A pair of animals were grown to a mean weight of 125 g and then were starved. Body weight and egg production were monitored until they died.

Results.

The energy contents of the various biological substances appropriate to this study are shown in Table 3. The caloric content of the algae varied and was determined monthly for U. lactuca (Figure 29). In general, the caloric content followed the same trends as did algal density; i.e., both were lowest in the summer and highest in mid-winter. Whenever conditions were "favorable" there was a dense algal crop and the algae were rich in energy. Caloric values of samples of U. reticulata were assayed four times during the study and appeared to follow the same seasonality as U. lactuca (Figure 29). The caloric values for U. lactuca were comparable to the values given for U. fasciata by Carefoot (1967a). Seasonal variation in caloric content of algae is well known (Paine and Vadas, 1969; Medcalf, et al., 1975; and Himmelman and Carefoot, 1975).

Since the studies described here parallel much of the work of Carefoot (1967a,b), his energetic figures are also shown in Table 3. Most of the values are in close agreement and the caloric value for U. fasciata fall within the range of values for U. lactuca. The only large discrepancy between the two studies is for the energy content of fecal material. It is possible that some of the difference between the two figures was due to differences between the algae, although it seems more likely due to procedural differences.

Respiration.

As a rule, rates of physiological processes can be expressed as a power function of body weight (von Bertalanffy 1960). There is a well

Table 3

Energetic Constants for Tissue, Spawn, Feces and Food of *A. juliana*
Numbers in Parenthesis Indicate the Number of Determinations

	Mean %* Dry Wt.	Range of Values	Mean Caloric Value Cal/Dry g	Range of Values	Mean % Ash	Range of Values	Cal/g (ash free)
Tissue	8.6 (25)	6.7 - 11.0	3036 (6)	2855-3470	38.0 (3)	32.8-42.03	4896
Spawn	10.2 (4)	9.4 - 11.3	3532 (3)	3333-3733	29.3 (3)	27.4-30.6	4966
Feces	--	--	968.3 (3)	930.8-996.7	68.4 (2)	69.0-67.8	3066
U. reticulata	21.2 (4)	20.4 - 22.5	variable	2248-3229	23.5 (3)	19.9-24.1	2939-4221
U. lactuca	20.1 (4)	19.0 - 21.6	variable	1869-3169	31.1 (15)	23.3-38.0	2712-4600
From Carefoot (1967)							
Tissue	9.05	--	2492	--	35	--	4811
Spawn	9.1	--	3036	--	38	--	4897
Feces	--	--	2111	--	47	--	3968
U. fasciata	18	--	2832	--	28	--	4029

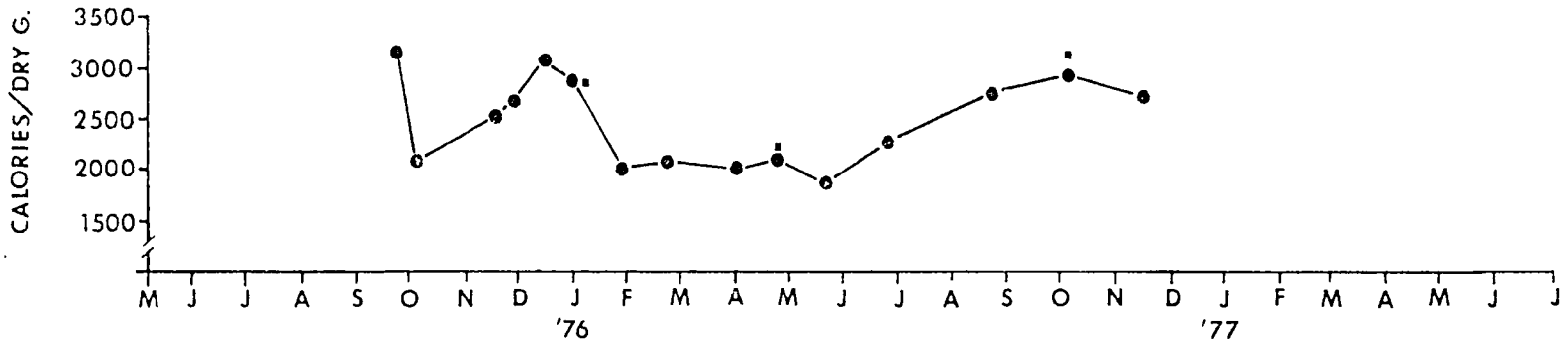

Figure 29. Mean caloric content of U. lactuca at Sand Island over a one year period. Squares indicate three values for U. reticulata from the same location. Ranges for mean values are shown in Table 11 (Appendix).

established relationship between oxygen consumption (Y) and body weight (x), taking the form $Y = AX^B$ (Zuethen, 1947; Prosser and Brown, 1961). This is more conveniently expressed logarithmically as log Y = log A+B log X. The value of the regression coefficient B has received much attention and Hemmingsen (1960) suggested that a value of .75 may be general for poikilotherms. The data for A. juliana with a coefficient of .787 are in good agreement with this (see Figure 30). One can estimate the respiratory rate of an animal of any size from this line.

Energetic Analysis of Animals under Ad libitum Feeding Conditions.

There are a multitude of ways of expressing energetic data. When one measures food ingested, growth, fecundity, feces, and metabolic rate, the number of relationships that can be made approaches absurdity, especially when one has the choice of expressing them as absolute numbers, rates, or percentages, and as a function of age, or a function of size, etc. In the following analysis the energetic data are expressed in a manner which seems most appropriate for understanding the energetic strategy of this species in the field.

An experiment where five A. juliana were fed U. lactuca ad libitum was chosen for detailed energetic analysis. Methods for this experiment are described in Chapter II and growth of the animals is shown in Figure 5 (Chapter II). Figure 31 shows feeding rate as a percentage of body weight. The sea hares consumed large amounts of food especially during the early stages when they were growing fast and laying large numbers of eggs. This capacity for food processing is very important

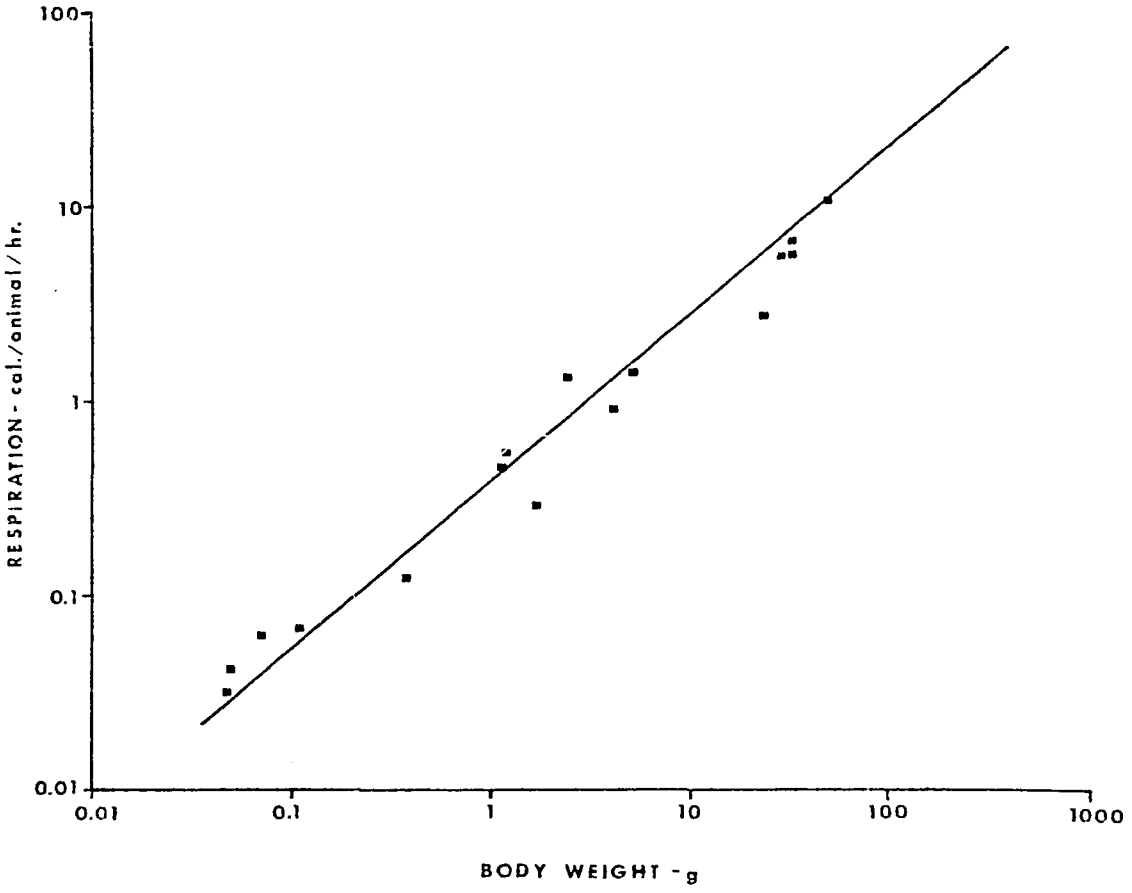

Figure 30. Respiratory rates in relation to body size for A. juliana. Animals were laboratory reared.

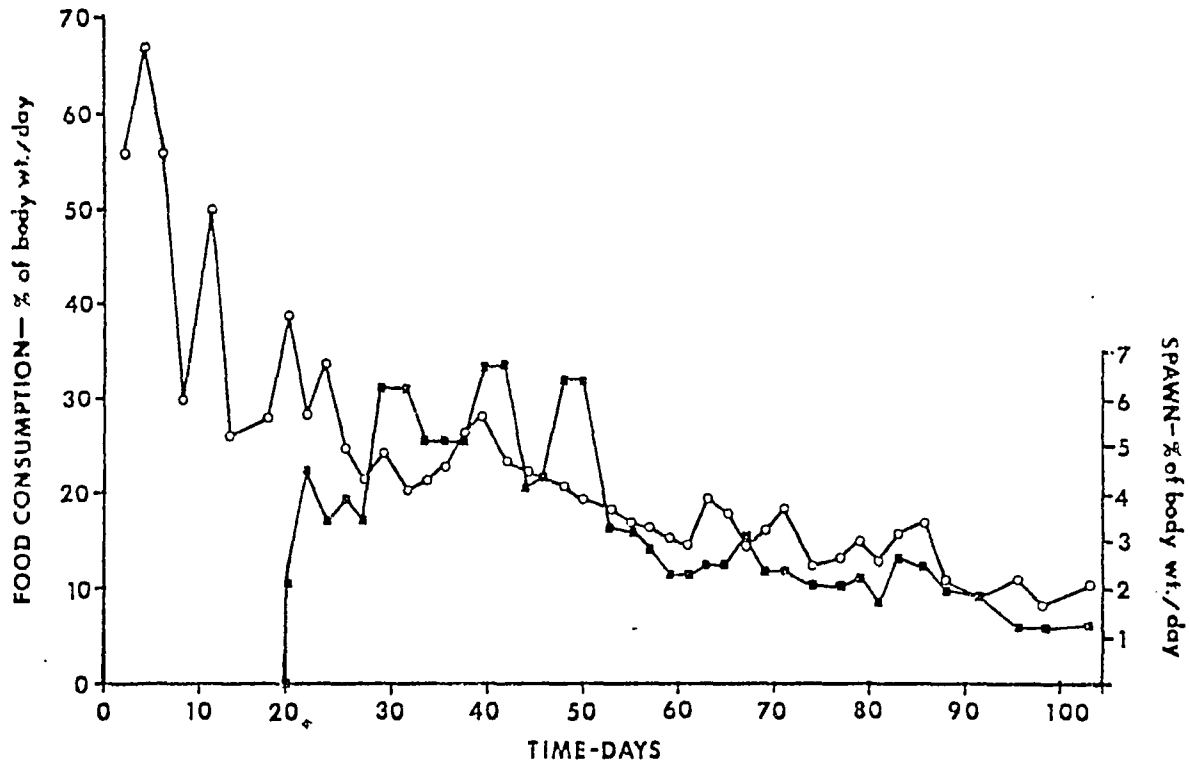

Figure 31. Food consumption and relative spawn production in a group of A. juliana fed ad libitum on U. lactuca. N = 5 animals.

to an animal whose growth and fecundity are so closely linked to the amount of food it eats.

The large amounts of energy consumed by a growing animal can be channeled into: 1) somatic growth, 2) reproduction, 3) maintenance, or 4) waste. Food eaten, weight gained and eggs laid were converted to calories using the values listed in Table 3. Caloric value assigned to the algae was an average of the values measured for U. lactuca at Sand Island during the time of the experiment (2274 cal/g). The amount of energy consumed which was allocated to somatic growth and spawn production combined can be considered as caloric gross growth efficiency (Figure 32). Efficiency was high in young animals and slowly tapered off as the animals aged. Both food consumption and efficiency declined as time went on resulting in a net decrease in energy available to the animal on a per gram basis.

When caloric gross growth efficiency was divided into growth calories and egg production calories, the energy trade-off between the two could be seen (see Figure 33). Energy to growth dropped very steeply when reproduction began. This energy trade-off was further illustrated by the fact that high peaks of egg production always correlated with low points for growth. The proportion of energy to egg production did increase slightly when growth ceased although the decrease in efficiency was lessening the available energy.

Since body weight increased while food intake as a percent of body weight and efficiency decreased, respiration took a higher and higher percentage of the energy budget as the animal aged. Figure 34 shows the percentage of ingested energy that went to respiration.

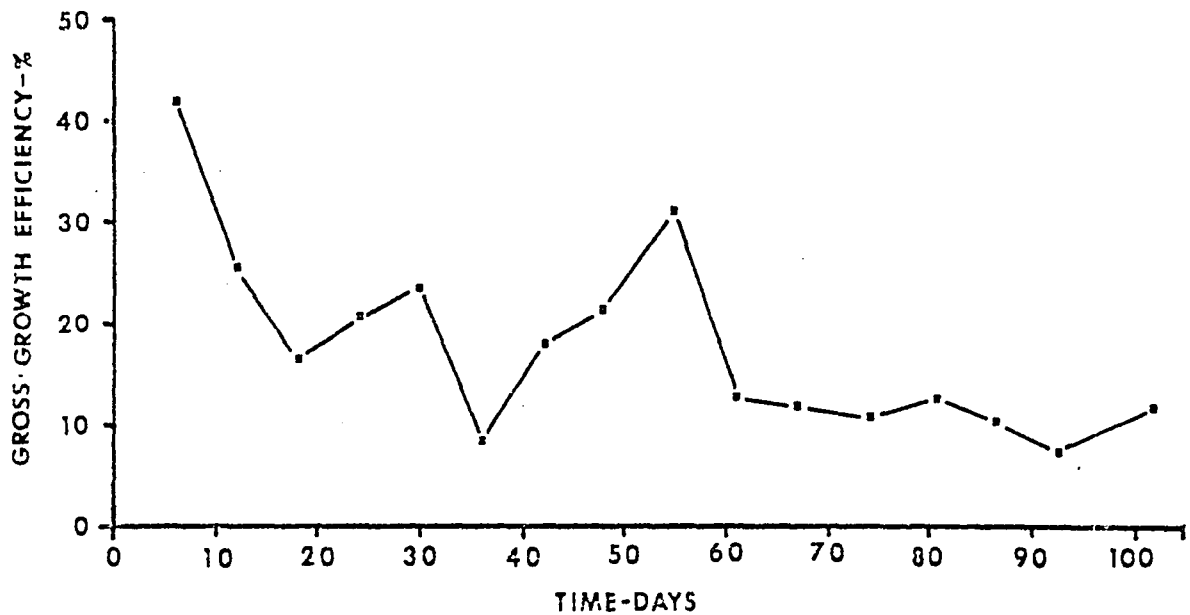

Figure 32. Caloric gross growth efficiency in a group of A. juliana fed ad libitum on U. lactuca. Efficiency measured as percent of ingested calories. N = 5 animals.

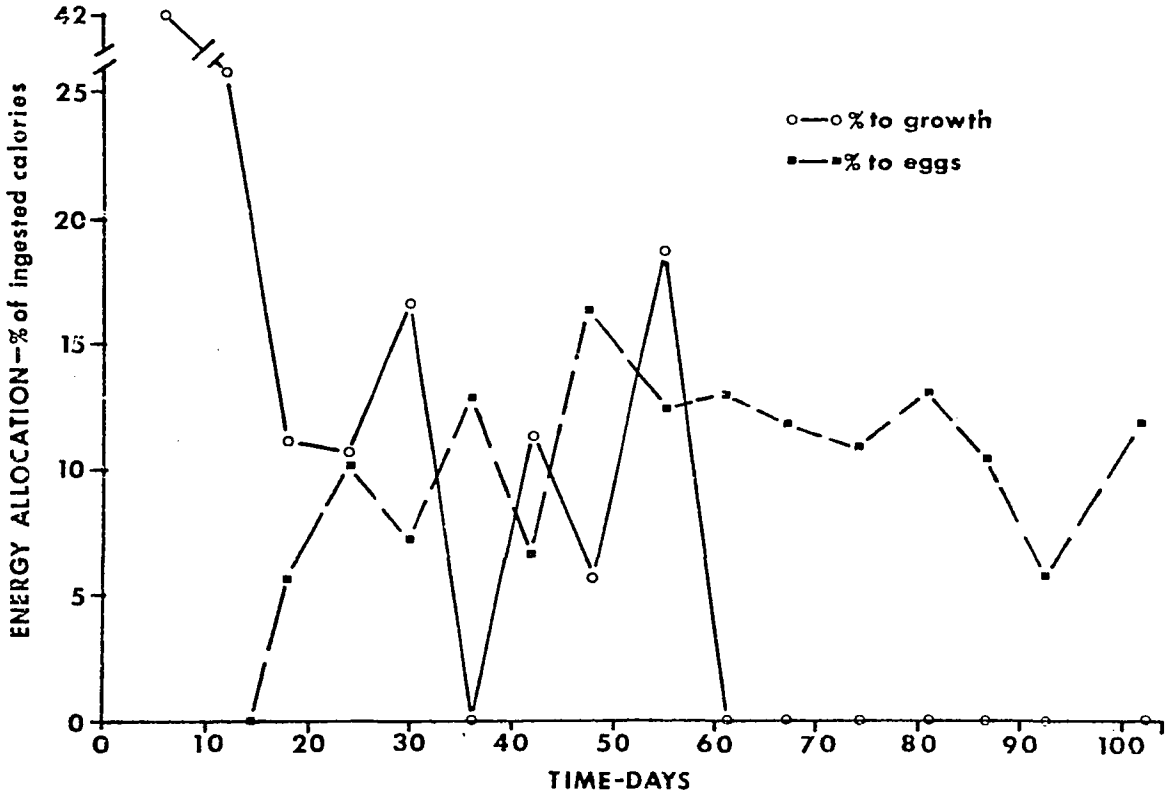

Figure 33. Energy allocation between growth and egg production in a group of A. juliana fed ad libitum U. lactuca. Allocation measured as percent of ingested calories. N = 5 animals.

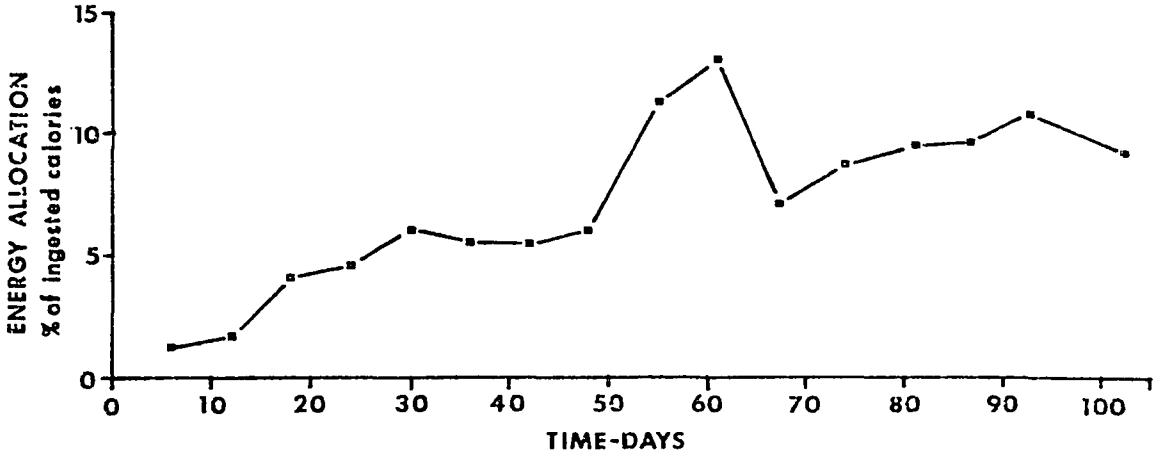

Figure 34. Percentage of ingested energy allocated to respiration for a group of 5 A. juliana fed ad libitum U. lactuca.

A total energy budget can be calculated by further analysis of this ad libitum feeding experiment. Table 4 shows the energy flow in animals fed ad libitum amounts of U. lactuca. A surprisingly high percentage, 46%, of the energy cannot be accounted for by the parameters studied in this experiment. Analysis of Carefoot's (1970) feeding data revealed that 38% of the calories ingested by A. juliana feeding on U. fasciata was unaccounted for. There were several ways energy could have been lost that were not measured in these experiments: (1) excretion of dissolved nitrogenous wastes, (2) mucus secretion; (3) increased metabolism due to increased activity; and (4) leakage of substances such as amino acids and small sugar molecules from the body. Judging from the copious amounts os slime these animals are capable of producing, this large amount of their energy to be lost to mucus secretion is reasonable. Teal (1957), Johannes (1967), and Calow (1974) have reported similar large energy losses to mucus production in other marine animals.

Energetic Analysis of Animals on Reduced Feeding Rations. Knowingly the energetic strategy of animals held in optimal conditions with ad libitum feeding is important, but animals in the field do not exist under such favorable conditions. The reduced maximum sizes observed in field animals were probably a result of limited access to food. Analysis of growth and energetic data from the food rationing experiments reveal how the animals' physiology adjusts to various levels of feeding.

The first rationed feeding experiment to be considered involved growing animals to sexual maturity under ad libitum conditions and then

Table 4

Energy Budget for Five Animals Fed *ad libitum* *U. lactuca* for 104 Days

		Per Animal	% of #1
1)	Total energy ingested (calories)	1,211,886	
2)	Total energy to respiration (calories)	129,050	10.65
3)	Total energy to reproduction (calories)	129,551	10.69
4)	Total energy to somatic growth (calories)	66,057	5.45
5)	Total projected energy to feces (calories)	330,635	27.28
	Sum of 2,3,4, and 5	655,294	54%
	Energy unaccounted for	558,391	46%

$$\text{Assimilation Efficiency} = \frac{\text{Calories Ingested-Calories of Feces}}{\text{Calories Ingested}} \times 100 = 72.7\%$$

$$\text{Growth Efficiency} = \frac{\text{Calories to Growth}}{\text{Calories Assimilated}} \times 100 = 22.2\%$$

$$\text{Dry Weight Efficiency} = \frac{\text{Somatic Growth + Spawn (Dry Grams)}}{\text{Food Ingested (Dry Grams)}} \times 100 = 10.95\%$$

$$\text{Caloric Gross Growth Efficiency} = \frac{\text{Somatic Growth + Spawn (Calories)}}{\text{Food Ingested (Calories)}} \times 100 = 16.14\%$$

placing some on rations of 10, 20, and 30 grams of Ulva per animal per two days (25, 50, 75% of body weight per two days). The methods for this experiment are described in Chapter III and the growth of these animals is shown in Figure 10 (Chapter II). The necessary computations were made to convert the amounts of food consumed, spawn produced, weight gained and respiration into calories. These figures were tallied for the total life span and are shown in Table 5. The results indicate t hat within the range tested, food rationing does not alter the relative amount of energy that goes into reproduction and spawn production.

A second group of animals was fed 75% of the ad libitum rate from the time they weighed 2 grams. The methods for this experiment were described in Chapter II and the growth of these animals is shown in Figure 5. The energetic values for these animals and the ad libitum control group are shown in Tables 6 and 4. The rationed animals invested an equal amount of energy into reproduction and growth while those fed ad libitum invested twice as much to growth as compared to reproduction.

The third experiment dealt with animals which were grown to sexual maturity (40 g in this case) ad libitum and then placed on a maintenance ration of 4 g of U. lactuca per two days per animal (10% of their body weight per two days). These animals ceased growing but continued to lay eggs (see Figure 13, Chapter II; and Table 7). All of the energy above maintenance costs was allocated to egg production.

The pair of animals which was grown to 125 g and then starved continued to lay eggs until the day they died at the cost of losing 80 g

Table 5

Energy Budget (per animal) for Three Groups of Five Animals Fed *ad libitum* on *U. lactuca* until Sexual Maturity and Then Put on Rations of 10, 20, and 3 g of Algae per Two Days

Feeding Regime (g/2 days)	Eggs Laid (g)	Eggs Laid (Dry g)	Eggs Laid (calories)	Food Eaten (g)	Food Eaten (Dry g)	Food Eaten (Calories)	Weight Gain (g)	Weight Gain (Dry g)	Weight Gain (Calories)
10	35.75	3.65	12,892	451	90.65	212,220	67	5.76	18,793
20	51.4	5.24	18,508	841	169.0	395,496	95	8.17	26,110
30	95.2	9.71	34,296	1,231	247.4	578,771	140	12.04	37,859

	% Calories to Eggs	% Calories to Growth	Caloric Gross Growth Efficiency (%)
10	6.07	8.86	14.9
20	4.68	6.60	11.28
30	5.93	6.54	12.47

Table 6

Energy Allocations to Spawn and Somatic Growth for Animals Fed *U. lactuca* at 75% of the *ad libitum* Feeding Rate. N = 5 Animals

Calories Ingested	% to Spawn	% to Somatic Growth	Caloric Gross Growth Efficiency
248,374	7.25	7.35	14.6

Table 7

Energy Allocation in Seven Feeding Studies on *U. lactuca*

Feeding Schedule	Food Eaten (wet g)	Size Attained (wet g)	Eggs Laid (wet g)	Fecundity % of max. Weight	Fecundity % of Cal. to Eggs	% of Calories to Growth
.5 g/day from a weight of 2 g	56.6	8.5	5.25	61.7	7.33	8.6
75% of *ad libitum* rate from a weight of 2 g	543	70	50	71	7.25	7.35
ad libitum to 40 g then 2 g/day*	237	36.4	25.6	70	9.23	9.5
ad libitum to 40 g then 5 g/day	451	67	38	53	6.07	8.86
ad libitum to 40 g then 10 g/day	841	95	51	54	4.68	6.6
ad libitum to 40 g then 15 g/day	1231	140	95.2	68	5.93	6.54
ad libitum from 2 g	2651	267	360	135	10.69	5.45

*The figures for this study were extrapolated to equal 102 days. The rest of the studies lasted from 102 to 104 days.

of body weight apiece in 15 days. Their growth and egg production is shown in Figure 35. A little over 14% of the calories from the lost body weight sent into egg production.

Analysis of the experiment in whicha pair of animals was fed the small ration of .5 g of U. lactuca per day revealed that even though these animals grew only to a maximum size of about 8 g, they still laid several egg masses which totaled over 65% of their final body weight.

Chronological and Physiological Age. Animals which were fed ad libitum or constant rations showed similar energetic patterns: relatively high rates of feeding, growth, and reproduction which slowed as they aged. But this is not always the case as was shown in the experiment where animals were grown to sexual maturity, fed ad libitum, then put on a ration of 10% of their body weight per two days for seven weeks, and then returned to ad libitum feeding. Their growth is shown in Figure 13 (Chapter II).

As was discussed earlier, many physiological processes are a function of size and not age. Even though the animals in the above experiment were of a chronological age in which they would normally have long since stopped growing, they were still of the young physiological age that corresponded to their size. And they still had the capability to grow at the rate characteristic of their size. Figure 36 shows the increase in relative egg production after they were transferred from a maintenance ration to an ad libitum food supply. Not only do they resume growth, but also egg production responds to an increase in food

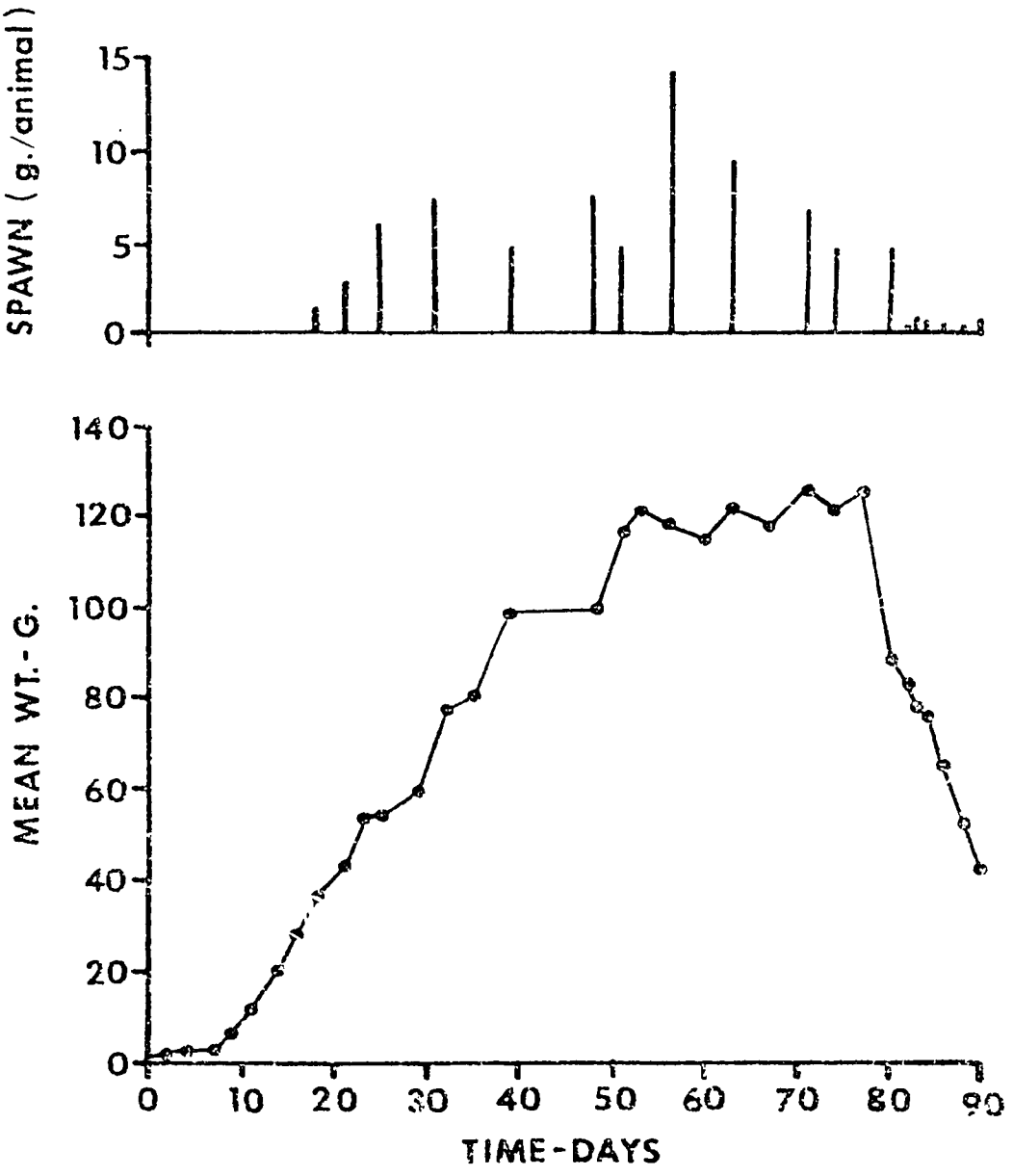

Figure 35. Growth and spawn production of a pair of A. juliana grown to 125 g on U. reticulata and then starved.

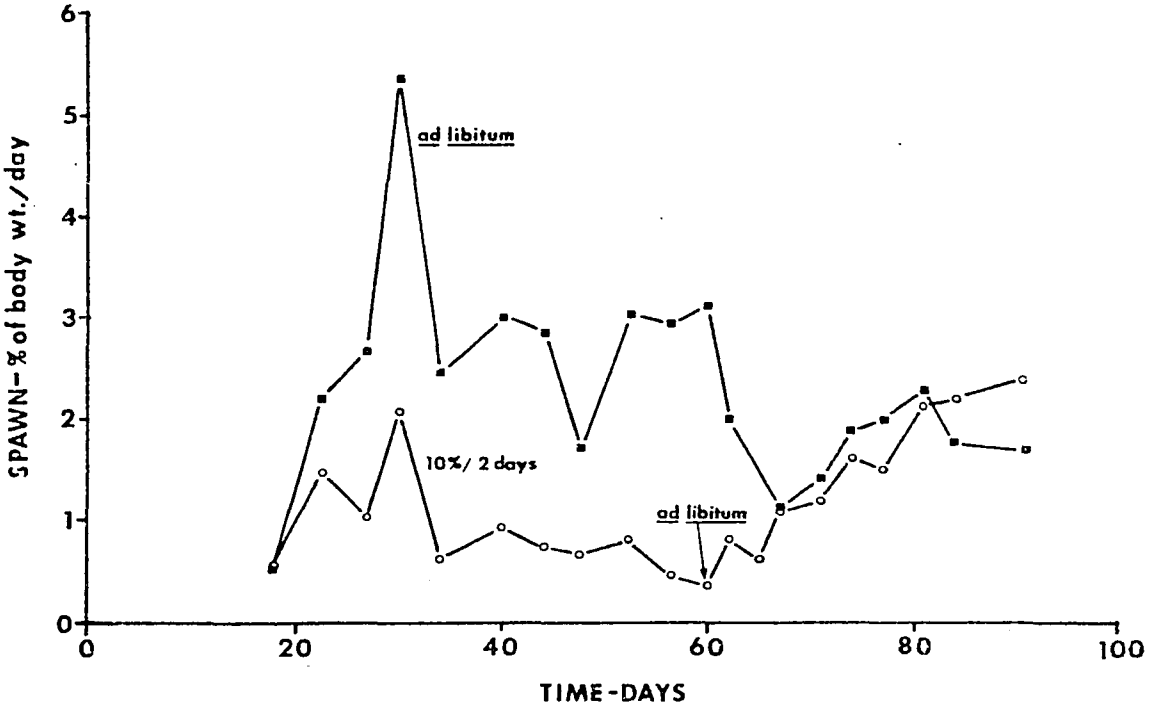

Figure 36. Mean relative spawn production of two groups of A. juliana. One group was fed ad libitum throughout the experiment. The other was fed ad libitum until sexual maturity, then placed on a maintenance ration of 10% of their body weight per 2 days, and then returned to ad libitum feeding at 60 days. Control group contained 5 animals and the rationed group contained 4.

availability even after extended periods without growth and with low egg production. Undoubtedly there is a limit to how long an animal can retain its ability to respond to more favorable conditions such as this. An animal that has begun to senesce will not respond to increased food the same way that a younger animal will. The ability to resume growth probably declines constantly during the entire period that an animal is nutritionally held in a no-growth state; the rate of decline is, however, much lower than in an animal that is rapidly growing. The importance of this in relation to animals in the field is that, if adult animals are small and not growing, it is because they do not have access to a sufficient amount of food to promote growth, and not because they were stunted by insufficient feeding at some prior time.

Application of Laboratory Feeding Studies to Animals in the Field. One of the purposes of the rationed feeding experiments was to obtain a method for estimating feeding rates of animals in the field. Animals in two laboratory experiments displayed growth patterns which resembled those observed in the caged animals in the field and the spotted animals released at the Sand Island site. The animals which were grown to sexual maturity under ad libitum feeding and then fed a ration of 10% of their body weight per two days maintained their weight while still laying eggs as did the animals fed at 75% of the rate of ad libitum fed animals. In 2-1/2 to 3 months, the estimated life span for A. juliana in the field, the 75% ration animals ate about 430 to 485 g of Ulva, laid 40 to 45 g of eggs, and maintained a weight of around 60 g. The animals

which were fed ad libitum to maturity and then 10% of their body weight per two days ate 140 g of food and laid 5.23 g of eggs while maintaining a weight of 35 g in the same period of time. In 10 to 12 weeks animals grown in the cage laid 65 to 80 g of eggs apiece and maintained weights of about 55 g. Animals outside the cage seemed to lay eggs at about the same rate as those in the cage (2.23% of their body weight per day).

Rationed animals in the laboratory laid fewer eggs than those in the field relative to their body weight. Since these experiments were done in sea water tanks located inside the building, it is possible that reduced light levels caused lower rates of egg production. The ambient light vs. dark experiments discussed in Chapter II showed how lowered light levels can reduce the energy input to egg production. Even though the animals in the dark grew to more than twice the size of animals maintained in ambient lighting, they laid fewer eggs.

From the results of the experiments with the caged animals in the field and the size distributions at Sand Island, one can estimate feeding rates for animals in the field. An animal growing to 35 g in the field, with a 10 to 12 week life span, produces about 40 g of eggs. The laboratory feeding experiment where the animals were fed ad libitum to sexual maturity and then placed on a 10% of their body weight per two day feeding ration best approximated this field growth pattern. From the data of this laboratory experiment one can estimate the feeding rate of those in the field. The laboratory-reared animals did not lay as many eggs as those in the field so the appropriate amount of extra energy has to be added to the diet to increase the total egg production

to 40 g. Assuming a 22.3% wet weight conversion efficiency, this would mean an extra 152 g of Ulva for a total of 292 g of algal food. Thus, the projected life history for this theoretical animal in the field would be: attainment of sexual maturity at a weight of 30 to 35 g at an age of six to seven weeks post-settling; a fecundity of .81 g of eggs per day for seven or eight weeks; and a total food consumption of 292 g of Ulva.

A field population would be consuming on the average 11% of its total weight in food per day and laying about 2.3% of its weight in eggs. At times of high population density at the Sand Island site, this translates to over 11 kg of algae eaten per day and just under one trillion eggs produced every day.

Discussion.

It is advantageous for animals such as A. juliana, which sustain high mortality rates as juveniles, to spend as little time as possible in these early stages. In fact, by the time these animals have reached two or three grams, they have left their juvenile habitat where physical factors cause high mortality, and have become too large for most of their predators. The extremely high feeding rate and rapid growth of juvenile A. juliana reflect the strength of these selective pressures. Paine (1965) reported that Navanax inermis can also escape a significant source of mortality, canabalism, by growing to 20 g or larger. Paine (1976) also showed that mussels escape predation by attaining large size.

As the aplysias approach sexual maturity, energy must be diverted in large amounts from growth into processes related to reproduction. The relative amounts of energy that go into growth and reproduction are dependent upon the amount of food available to the animal and on the animal's physiological age. Addressing this problem, Spight and Emlen (1976) stated, "An unpredictable food source is a major adaptive challenge to any organism as it seeks to maximize its production of gametes. An individual that can readily adjust its fecundity to the food supply should be able to produce more offspring and thereby will gain a significant advantage over those that cannot adjust. Consequently, techniques for adjusting fecundity should be major elements of a species' strategy". They went on to outline two strategies that could be employed to take advantage of an increasing food supply: (1) allocating

the extra energy directly into gamete production, and (2) investing the extra energy into growth and thus increased fecundity since larger animals have larger clutches. These hypotheses assume the absence of other selective forces acting upon animal size. A species which becomes reproductively active once a year can only respond to an increase in food by growing. Conversely, animals with determinate growth can only channel extra energy into reproduction.

A. juliana which lays eggs every few days, should be capable of reacting to food increases in either way. There is no doubt that individuals of this species grow larger with an increase in food supply and that they are capable of this growth at any time in their lifetime. This growth in turn results in larger egg masses and thus higher fecundity. Whether or not these animals actually have a higher rate of fecundity is a more complex question. Fecundity rate must somehow take animal size into consideration.

There are two ways to express fecundity as a rate. The first is to calculate it as the weight of spawn produced relative to the weight of the animal. The other, more energy based approach, is to express fecundity rate as the percent of calories ingested that are allocated to producing eggs. Both are valid procedures, each addressing different questions. Both relationships were calculated from data measured for A. juliana and the resulting values are shown in Table 7. Whether reproductive effort was defined as weight of eggs laid as the percentage of maximum weight or as the percentage of ingested calories that went to reproduction, the same trends were evident: reproductive effort is

high at the lowest rations, drops at moderate feeding levels, and rises to the highest value when animals are fed ad libitum.

Aplysia juliana can adjust its fecundity to a varying food supply both by increasing its size and consequently its clutch size, and by changing the proportion of its ingested energy which is allocated to reproduction. The response of increasing size with more food has a much greater effect on fecundity than does the change in energy allocation. An increase in size allows an animal to process more food in a given amount of time and since this animal seems to be limited by its access to food rather than by its abundance, the increase in processing capacity would be more effective. This priority for growth is shown by the fact that in every case except the ad libitum feeding situation the proportion of energy that went into growth was higher than that to spawning. Once animals have begun laying eggs, they will continue, regardless of how much food they have available. Producing some eggs, even if only a small number, seems to have top priority in the energy strategy of A. juliana. If animals are starved they will still lay eggs and if they are fed just enough to prevent weight loss, they will still lay eggs. At very low rations, egg production is favored over weight gain if animals are sexually mature. At higher feeding levels both growth and egg production will be supported about equally, and as animals are supplied with more food approaching ad libitum conditions, a higher percentage of ingested energy will go into reproduction. Underlying, and additional to these rationing effects, is the shift in energy allocation as the animals age. Before maturity

all energy above maintenance goes to somatic growth; after spawning commences, energy in excess of that required for metabolism goes into egg production and growth; and later when the animals cease growing, all available energy goes into egg production (see Figure 33).

Different feeding rates often result in variation of digestive efficiency. As more food is "pushed" through the digestive tract, the efficiency often goes down. This has been shown in Daphnia magna (Ryther 1954), copepods (Cushing 1955), and sea urchins (Lasker and Geise 1954). The caloric gross growth efficiency of A. juliana did not vary much between the various feeding regimes, perhaps because of the ability of the digestive system to efficiently digest even large amounts of food, or the way the animals were fed. With all the experiments other than ad libitum feeding, the two day ration was all placed in at once and the animals fed on it until it was gone. This may have resulted in similar efficiencies to the ad libitum experiment since feeding was always at a maximum rate regardless of how much was ultimately available.

A. juliana produce large numbers of eggs during their life time. In many of the feeding experiments the weight of total eggs laid was equal to somatic weight and in the cage at Sand Island the aplysias laid almost double their maximum weight in eggs in four months. Hughes (1972) reported that the prosobranch Thais lapillus laid enough eggs in a year to equal 81% of its stored body energy. Spight and Emlen (1976) reviewed the gastropod literature and derived an average value for prosobranch egg production at 23 to 37% of the body weight per year. A total production figure will of course vary depending on how long the animal lives.

The most significant aspect of the fecundity of A. juliana is that it can lay twice its weight in eggs in only four months. These slugs do not put an unusually large proportion of their energy into reproduction, but since they process so much food large numbers of eggs can be produced.

An A. juliana reared in the laboratory produces most of its eggs early in its life before it reaches maximum size. The decline in egg production relative to body size with age is not a function of a smaller proportion of the energy being allocated to reproduction, in fact the trend is the opposite (see Figure 33). Instead, the reason for this drop in egg production is reduced feeding. As was shown in Figure 31, feeding rate relative to body size declines with age. Lowered feeding rate may be associated with the reduction in gross growth efficiency (see Figure 32). The drastic reduction in egg production for this species may only be seen in the laboratory since the life span in the field is extrapolated to be considerably shorter than that in the laboratory.

CHAPTER VI

Summary and Conclusions

Aplysia juliana lives and reproduces in a highly variable environment which is often disturbed by strong waves. Storm generated waves can overturn their rocky shelters and wash them away. Storms are also known to move large masses of sand and gravel into areas burying large parts of the Aplysia habitat in addition to tearing out much of the algal crop. Secondly, the quantity of food of A. juliana, species of Ulva, varies unpredicably in both space and time. During the three year course of this study, some locations have had crops of algae for just a few months and others have maintained algal populations for the majority of the time. In addition, the nutritional quality of the Ulva changes throughout the year.

Species living in such variable environments often have populations that contain relatively few individuals and are constantly changing in density (Erlich and Birch, 1967). Environmental fluctuations in the A. juliana habitat are large and frequent enough that the risk of local extinctions must be high.

Species for which some limiting, necessary resource is unpredictable in space and time, depend for survival on producing numerous offspring scattered widely in space and time (Sale, 1977). An individual A. juliana produces millions of eggs over an extended reproductive lifetime without regard to season. Further evidence for this strategy is that an Aplysia starts producing eggs very early in its life regardless of body size and will produce eggs even in the absence of

food at the expense of body weight. The asynchrony of high and low densities between locations keeps recruitment potential relatively stable and reduces the chance of total species extinction over wide areas. The constant prolonged production of larvae maintains recruitment pools which may be analogous to stable refuge populations described by Connell (1970), Kitching and Ebeling (1967), and Paine (1974).

Stearns (1976) has summarized theories on life history tactics and noted that they all depend on examining, for any given species, a particular set of life history traits. They are brood size, size of young, age distribution of reproductive effort, the interaction of reproductive effort with adult and juvenile mortality, and the variation of these traits among an individual's progeny. Particular sets of these traits have been assembled as correlates in supposed particular, evolutionarily selected reproductive strategies usually referred to as r- and K- selection. Much controversy has developed over the r-K selection hypotheses (see Stearns, 1976; Pianka, 1970, 1972). However, as Gadgil and Solbrig (1972) pointed out, r- and K-selections are relative terms and should only be used to compare similar organisms and Pianka (1970) emphasized that species occur within an r- to K- continuum. The application of these hypotheses to animal species should not be an end in itself. They should be used as criteria for examining characteristics of the life history of species that will allow comparison of that species with other closely related species. Viewing animals within this framework can be very informative.

By Stearns' (1976) definition this species is semelparous because it has only a single unbroken reproductive period and seems to fit the "annual habit" better than the "perennial" one. However, Aplysia does not fit this definition precisely because an individual can still be producing larvae long after its earlier progeny have settled, grown and started producing their own. For this reason, A. juliana might be better thought of as iteroparous.

A second question deals with the relative rates of juvenile and adult mortality. If planktonic larvae are considered juveniles, as it seems they would have to be, then it would be extremely rare to find a marine animal in which adult mortality rates are higher than juvenile ones. In the case of A. juliana the decision is not too critical however, because whether or not the larval stage is considered, pre-reproductive mortality rates are still much higher than post-reproductive rates.

Aplysia juliana still conforms to many of the criteria compiled by Stearns (1976) for an r- selected species. It has population of variable sizes which frequently become extinct and require recolonization, a short life span, many small young, high reproductive investment, and it lives in a harsh environment. The features which fit the criteria for a K- selected species are uncertain juvenile survival (adult survival is also uncertain but not to the same extent), relatively large body size, iteroparity, and many aspects of its "climate" are constant.

The life history of A. juliana incorporates two characteristics which maximizes reproductive effort. First is the fixed time to

sexual maturity. The growth during this time is limited by food abundance, therefore their size at sexual maturity and thus their reproductive capacity is closely matched to the food supply. Secondly, they retain their growth potential so size and fecundity can change with increased food.

There are some further energetic considerations which reflect this species' life history strategy. Cohen (1971) predicted that when conditions are uncertain, the optimum tactic is to divide available energy between reproduction and somatic growth. This ensures that at least some offspring are produced while energy is also invested in growing larger on the chance that an animal will live to reproduce again, this time at a larger size. That habitat conditions for A. juliana are temporally uncertain and unpredictable is reflected by the fluctuations in its population densities and its frequent population disappearances. The resulting adaptive tactic is that individuals begin reproducing early by dividing energy between growth and reproduction. Individuals of a species which delays reproduction until large sizes are reached, can lay much larger clutches, but also risk dying without reproducing at all. Aplysia juliana "hedges its bet" by starting to reproduce young while maintaining the capacity to grow.

According to Williams (1966a, b), reproductive effort should increase with age because reproductive value decreases with age. Whether A. juliana conforms to this generalization depends on the definition of reproductive effort. The most rigorous definition of reproductive effort is the percentage of energy consumed that is

allocated to reproduction. In this framework, the reproductive effort in A. juliana stays more or less constant even though egg production as a function of body size drops very low as an animal ages (see Figure 36, Chapter V).

The life history of A. juliana maximizes sheer numbers of offspring. This emphasis on quantity of offspring suggests the strategy is to saturate the plankton with larvae and in this way be able to take advantage of periodic favorable habitats in its highly unpredictable environment.

APPENDIX

Table 8

Standard Deviations for Mean Weight Shown in Figure 10

Food Ration	10g of *Ulva*/2 days Mean Wt	--S.D.	20g of *Ulva*/2 days Mean Wt	--S.D.	30g of *Ulva*/2 days Mean Wt	--S.D.
Date						
11/14	40.0	1.34	40.4	7.09	41.4	5.48
11/16	32.6	6.15	34.6	3.4	35.2	4.23
11/20	33.9	5.47	34.1	3.68	47.3	7.03
11/22	33.8	4.85	41.7	2.72	51.5	7.92
11/24	43.9	5.44	49.6	2.68	67.1	6.91
11/26	41.1	7.61	50.8	4.98	64.1	13.88
11/28	44.1	5.98	51.3	3.38	65.5	12.5
11/30	45.7	7.0	59.6	5.23	83.3	14.07
12/2	47.8	7.12	66.9	2.43	96.9	15.22
12/4	53.2	7.27	72.1	6.63	96.78	19.43
12/6	49.9	11.91	72.5	5.66	100.6	17.57
12/10	56.9	5.05	80.6	3.32	117.5	20.85
12/12	56.4	6.44	76.48	7.77	111.7	17.4
12/14	68.9	6.11	82.1	6.0	112.9	10.63
12/18	67.1	6.46	91.85	12.41	136	22.69
12/20	65.7	7.28	90.7	11.86	140.7	27.43
12/24	68.9	7.87	89.9	10.56	133.8	25.4
12/26	66.87	6.8	96.4	13.1	127.8	25.26
12/28	67.7	6.21	98.7	9.3	132.2	26.2
12/30	64.33	6.62	93.43	13.45	138	24.0

Table 8, continued

Food Ration	10g of Ulva/2 days Mean Wt--S.D.		20g of Ulva/2 days Mean Wt--S.D.		30g of Ulva/2 days Mean Wt--S.D.	
Date						
1/3	69.57	6.27	97.5	9.68	141	20.45
1/5	68	7.56	15.45	10.04	150.3	29.06
1.7	69.2	6.91	93.5	13.95	147.5	26.1
1/9	68.27	7.05	92.03	11.41	132.3	28.87
1/11	65.1	7.48	91.38	10.43	132.3	22.49
1/13	65.3	8.2	91.85	10.4	132.3	21.8
1/15	68.7	4.7	91.15	12.3	136	21.66
1/17	65.9	15.9	97.3	11.4	142.6	21.2
1/19	67.3	6.5	91.5	11.7	135	22.4
1/21	56.6	15.0	91.1	11.9	137.8	25.2
1/23	57.6	13.6	99.1	11.1	147	25.8
1/29	72.5	only 2 left	120.6	22	166	35.6
1/31	61.8		95.45	11.6	133	30.07
2/2	64.8		92.48	11.55	145	26.7
2/6	73.9		91.8	10.67	138.2	31.5
2/10	77.25		100.9	9.57	138	28.3
2/14	70.75		93.5	14.0	139.3	25.8
2/20	72.4		104.1	9.6	135.4	23.1
2/22	72.45		94.9	12.87	133.4	23.95
2/24	64.2		94.2	9.96	145.6	19.9
2/28	67.5		96.4	11.9	133.0	19.99
3/2	70.7		92.8	10.0	136.8	21.2
3/4	74.6		91.4	9.57	142.0	22.1

Table 8, continued

Food Ration	10g of Ulva/2 days Mean Wt--S.D.		20g of Ulva/2 days Mean Wt--S.D.		30g of Ulva/2 days Mean Wt--S.D.	
Date						
3/8	73.9		89.77	8.4	146.5	16.9
3/14	68.0		97.7	11.96	131.5	20.9
3/16	64.0		102.2	12.2	140.1	18.9
3/18	69.7		99.3	11.9	125.7	14.2
3/22	81.1		105	7.96	150.2	25.5
3/24	72.1		97.6	8.7	136.7	11.7
4/17	69.0		100.33	6.8	130.5	16.9

Table 9

Ranges in Weights for Five *A. juliana* fed *ad libitum* *U. lactuca*

Day #	Range (g)	Day #	Range (g)
0	.91-1.1	48	168.7-220.6
2	2.95-3.26	51	144.7-208.8
4	6.07-8.09	53	149.6-212.5
6	15.9-19.05	55	213.8-275.3
8	17.0-21.12	57	177.3-225.8
10	33.4-41.7	59	208.3-267.6
12	35.5-50.8	61	202.3-275.5
14	52.8-66.7	63	213.0-260.0
16	50.32-66.2	65	219-276
18	63.2-71.75	67	203-282
20	64.01-89.29	69	225-279
22	69.4-96.2	71	201-256
24	75.5-109.5	75	195-240
26	94.6-119.5	77	213-258
28	81.1-114.6	79	196-252
30	112.5-149.7	81	216-271
32	93.3-143.9	83	251-282
34	105.0-153.2	87	200-247
36	98.1-138.5	89	231-274
38	123.4-172.0	93	199-240
40	109.3-154.9	96	191-241
42	142.8-186.5	98	191-243
44	145.2-213.4	100	193-235
46	164.7-213.0	103	188-262
		105	197-250

Table 10

Animal Weights for A. juliana fed ad libitum U. reticulata. N = 2

Day #	Animal Weights	Day #	Animal Weights
0	.25,.19,.22	62	91.2,140
1	.64,.71,.57	64	158,120
5	2.29,2.28,2.37	67	97.5,181
8	3.57,3.69,3.79	71	176,130
13	6.7,6.86,7.75	73	182,141
15	7.93,8.48,4.69	75	129,181
17	11.81,13,22	77	140,163
19	18.81,16.22	80	198,128
21	21.51,22.87	84	143,167
23	32.94,29.67	87	130,190
26	25.06,29.04	90	190,124
28	26.15,30.45	93	147,218
30	34.72,27.2	96	175,108
33	37.29,36.45	98	197,131
35	44.5,35.49	101	193,113
37	54.39,34.2	103	112,177
39	69.61,69.23	106	201,129
41	71.53,42.27	109	117,166
43	57.92,71.3	111	138,210
45	102.6,76.0	115	225,127
47	112,87.6	118	198,162
49	110,88.1	121	130,198
53	106,74.7	124	247,134
55	113,83.1	127	197,123
57	131,84.9		

Table 11

Caloric Values for Replicate Samples of Algae at Sand Island

Algal Species	Date Sampled	Replicate Values (Cal/dry g)
U. lactuca	9/25/75	3273,3117,3145
U. lactuca	10/1/75	2417,2386,2142
U. lactuca	11/23/75	2596,2493
U. lactuca	12/2/75	2732,2604
U. lactuca	12/16/75	2827,3321,3108
U. lactuca	1/1/76	2950,2802,2861
U. lactuca	1/29/76	2016,2159,1865
U. lactuca	2/24/76	2113,2427
U. lactuca	4/4/76	1779,2175,2092
U. lactuca	4/28/76	2002,2050,2313
U. lactuca	5/25/76	1836,1949,1822
U. lactuca	6/29/76	2589,2142,1822
U. lactuca	8/26/76	2742,2959,2510
U. lactuca	10/8/76	2992,2828
U. lactuca	11/23/76	2638,2926,2535
U. reticulata	1/1/76	2950,2802,2861
U. reticulata	4/24/76	2317,2297,2131
U. reticulata	10/8/76	3170,3661,2858

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